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THE FEEDING ECOLOGY OF THE RED-BILLED CHOUGH *Pyrrhocorax pyrrhocorax* L. IN WEST WALES, AND THE FEASIBILITY OF RE-ESTABLISHMENT IN CORNWALL

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A thesis submitted in candidature for the degree of
Doctor of Philosophy in the Faculty of Science
at the University of Glasgow

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April 1991

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Richard Mark Meyer

April 1991

"In a country so miniature as ours we perhaps have the vague general idea that we by now have the measure of all our native birds and animals. Yet what do we really see of them beyond an occasional fleeting glimpse? Most of their lives are spent invisible, private, beyond our range of understanding - how little we really know about them."

Kenneth Allsop

"A melancholy interest surrounds the Chough ... "

T.A.Coward

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SUMMARY

1. *The Red-billed Chough* Pyrrhocorax pyrrhocorax *is a protected species throughout the European Community and the rarest breeding crow in Britain. Its British and Irish population numbers* ca.*1000 breeding pairs, of which 2/3 are in Ireland. The present distribution is entirely confined to western maritime cliff regions, where there is a dependence on the invertebrate faunas associated with natural, semi-natural and pastoral habitats.*

2. *The study investigated the feeding ecology and habitat use of the Chough in Dyfed, West Wales, principally the county of Pembrokeshire, where there is low level population linearly distributed along the mainland coastline. Within Dyfed, the study region was separated into 4 blocks, with a variety of physiography and extending in all to >100km of coast. The study inquired into the decline of the Chough in Cornwall, its subsequent extinction as a breeding species in England in the 1970s, and the feasibilty of its possible re-establishment.*

3. *Ecological knowledge, acquired in the Welsh phase regarding habitat use and the biomass and diversity of the prey base, was applied in previously occupied sites in Cornwall in order to assess their suitability as re-establishment sites.*

4. *Assessment showed that the same suite of natural and semi-natural habitats exist in both regions, but precise examination of feeding areas showed that Chough usage is influenced more by fine detail of habitat composition which is not revealed by broad-based surveys. The existence of bare earth exposures within natural vegetation mosaics and annuals such as* Aira praecox *(Early hair grass) formed the most*

important single feeding complex that could be described botanically. Invertebrates associated with these complexes formed a key resource, in particular, ants during the breeding season.

5. Choughs using natural cliffscape showed better foraging success than those dependent upon pastoral agricultural systems. Cliff quality influenced agriculture usage, and, if high, reduced the significance of farming methods on adjoining land. However, it is unlikely that cliffs of high quality exist over a sufficient extent of coastline to support Choughs without recourse to pastoral agriculture. The Chough, for its long term survival, requires functional units which contain both natural and low intensity pastoral (=semi-natural) agricultural components.

6. Invertebrate faunas, notably beetles and fly larvae, associated with herbivore dung were used extensively throughout the year. The principal prey orders involved overall were Coleoptera, Oligochaeta, Diptera (mainly larvae), Hymenoptera, Crustacea, Arachnida and possibly Dermaptera.

7. Resources used in Welsh study areas existed at equal or greater levels in the Cornish areas examined, although management work might be required in order to increase the extent of suitably grazed semi-natural vegetation near proposed population centres, of which the Lizard emerged as the leading contender. Similar work is probably also necessary in Wales to increase viability within current ranges.

8. If re-establishment is to be attempted in Cornwall it should proceed as swiftly as possible, compatible with habitat requirements, to minimise the effect of deleterious recessive genes and reduced heterozygosity within the captive founder stock.

ACKNOWLEDGEMENTS

I approached this section with almost as much trepidation as I did all the others, not because it is not pleasurable to be able to thank people who have generously helped me but simply because so many have helped in so many ways that I know some will be omitted who really ought not.

I was funded principally by the Rare & Endangered Birds Breeding Centre at Hayle in Cornwall, and I wish to extend my very sincere appreciation to its Director, Mike Reynolds, his staff and all 'Friends' of *Operation Chough* for their warm support throughout and for taking on the costs after the initial impetus had come from Padstow Bird Gardens, where I first 'met' Choughs in Cornwall. For early indispensable support, I wish to thank Prince Charles (H.R.H. Duke of Cornwall), Dulverton Trust, Elmgrant Trust, Philip Radley Charitable Trust, Herbert Whitley Trust, Cornwall Bird-Watching and Preservation Society, Cornwall Trust for Nature Conservation, Cornwall County Council and RAF St Mawgan. Additional willing support came from the Nature Conservancy Council (as was) and the National Trust in Cornwall, both of which have a big role to play if the Chough is to recolonise Cornish cliffs. Derek Goodwin, author of *Crows of the World*, supported financially and offered friendly encouragement, for which I am very grateful.

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The research also took me to Brittany, where I made more good friends, in particular Alain & Annie Thomas and Maurice & Marie-Clare le Demezet; I look forward to returning and seeing their great efforts to protect their last few Choughs gaining ground.

Entomology seemed to play an increasingly big part in the project, and apart from those already mentioned, I should like to thank Helen Corrigan, Gerald Legg, Martin Luff, Alan Stubbs, Dick Loxton, David Sheppard, John Gregory, Peter Holmes, David Boyce, David Reed, Peter Elliott and especially Paul Buckland for expert help in identification.

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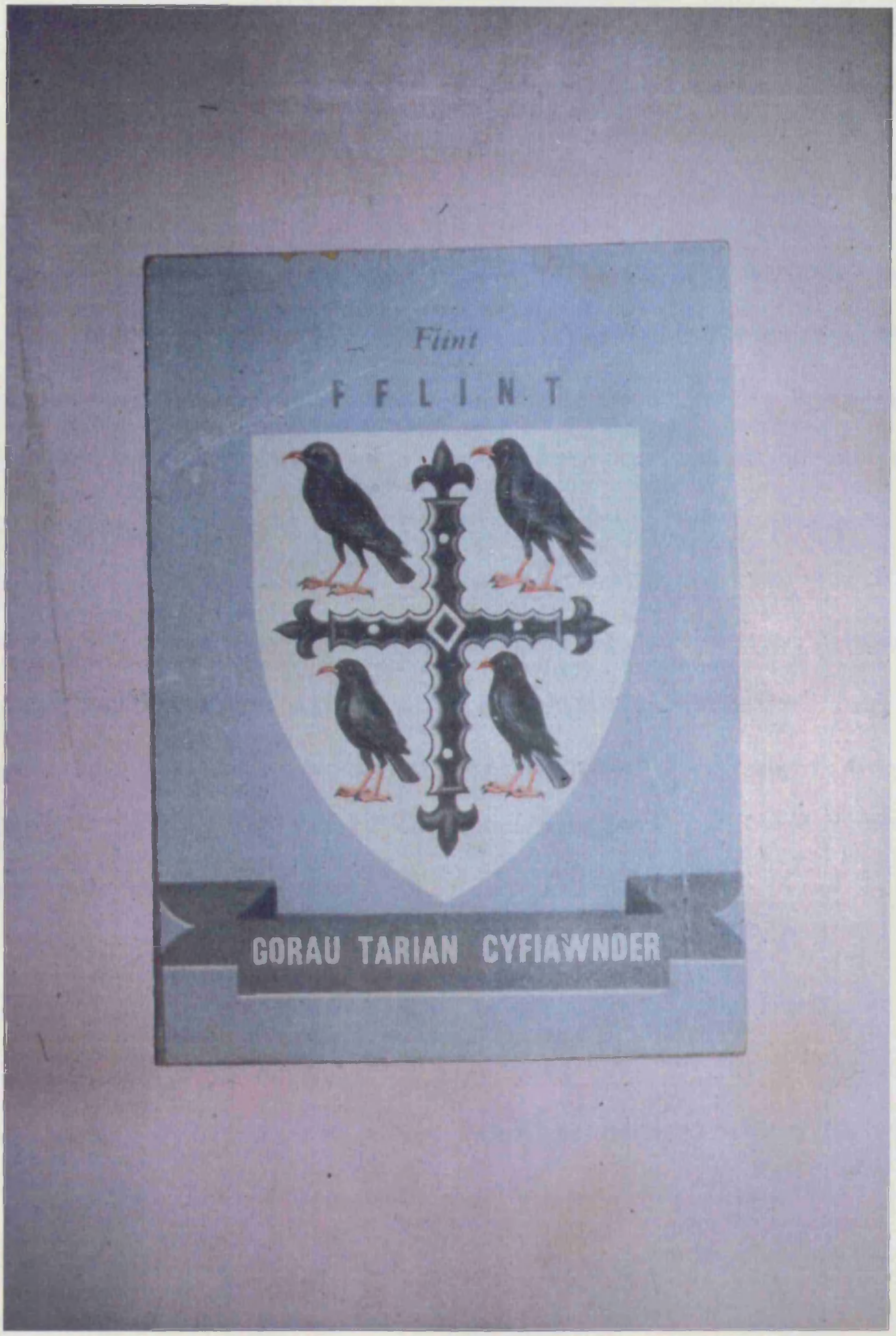
Finally, to all my family for their support throughout: Mij especially for her incredible patience and devotion, her parents, Jack and Peggy for their help in many ways. To Sally, Emma, Sam and Jojo for their unquestioning love, and to my parents for instilling in me an early love of wildlife and wild places. I was brought up in Flintshire, which has no cliffs and no Choughs although there are four on its coat of arms. I reckon they used to live where I lived - on the sheep-grazed limestone hills a couple of kilometres from the coast, and it still looks good for them today! My father had in his charge the Ancient Monuments in North Wales, and a very early memory is of a tame Chough kept at liberty at Caernarvon Castle by the custodian. It made a big impression, and to this day I treasure a lovely photograph taken by a friend of his of a Chough with nestlings at a slate quarry in nearby Snowdonia.

Frontispiece: Choughs feeding on sunny cliffslope near Cemaes Head in West Wales. The situation represents ideal feeding habitat.

Overleaf: Flintshire (now Clwyd) coat of arms.



Flint

FFLINT

GORAU TARIAN CYFIAWNDER

1 INTRODUCTION

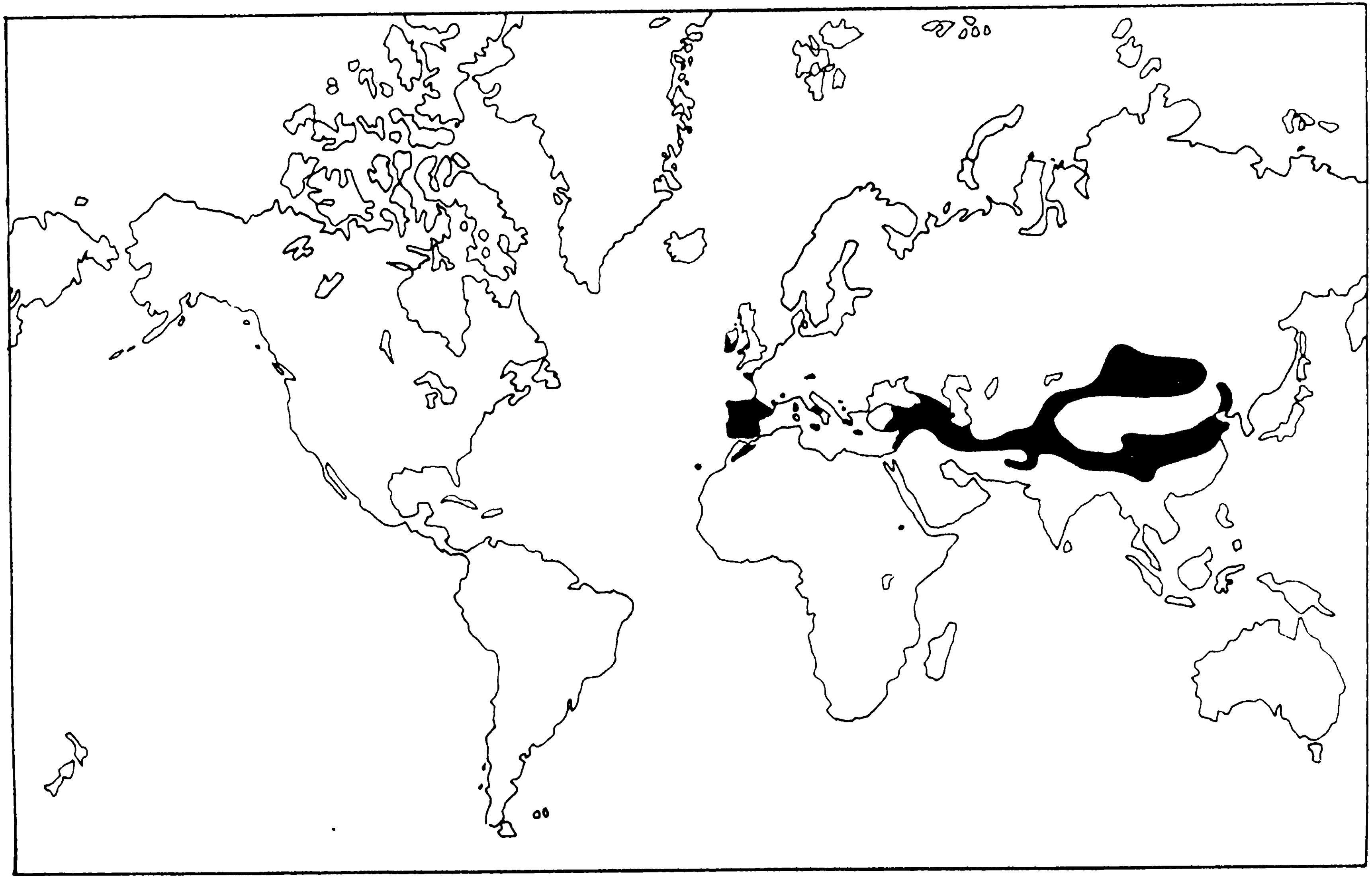
1.1 BACKGROUND PERSPECTIVE

The determinants of distributional patterns of animals are poorly understood and complex. In his recent critique, Wiens (1989) states that "the ecological suitability of a site from which a species is missing is not easy to determine, [and that] species often are absent from seemingly suitable sites within their geographical range". He further points out that "ecological tolerances of species dictate the environmental situations they occupy," and that "[e]valuation of habitat relationship has become an important part of wildlife and resource management". Trying to interpret the factors controlling the distribution of rare species is, therefore, likely to be a difficult, but important, area of conservation related research.

The Red-billed chough is the rarest member of the crow family (Corvidae) to breed in the British Isles. Many geographical races represent the species across a Palearctic range from the Mediterranean Basin in the west to the Far East (Dementiev & Gladkov 1951; Figure 1.1). Within Britain (Figure 1.2), the Chough is now absent from a substantial part of its former range. An understanding of the reasons behind the retraction of the Chough's range in Britain is central to any discussion of the causes of the change in status. Moreover, such an understanding may help

Figure 1.1

World range of Red-billed chough *Pyrrhocorax pyrrhocorax* (after Coombs 1978)



to explain the distributional pattern elsewhere, thereby assisting the conservation of the species. In the next chapter, I shall show why such conservation might have broader implications.

An isolated sub-population, amounting to <20 pairs, still survives in the Breton region of NW France (Guermeur & Monnat 1980; Figure 1.2). Vaurie (1959) recognised 7 subspecies and assigned the Breton population to the race *erythroramphus* of the Alps, Italy and Iberia, whereas Witherby *et al.* (1943) included it with the nominate race (a practice followed by recent authors). In Britain and Ireland, the distribution of the Chough now has a profound bias to some of the more rugged and remote sections of the west coast (1.3.2; Figure 1.2).

Until the early 1970's the nearest population to France was in Cornwall - approximately 80km across the English Channel (Figure 1.2). The last surviving wild Cornish Chough died in 1973 (B. Boothby, pers. comm.): the final act in a decline which had been occurring progressively in southern England throughout the C19 (Bullock *et al.* 1983a; see Section 3.4.2). Thus the retraction inclined northwards, with the population in SW ('West') Wales (Pembrokeshire) becoming the southern limit of the remaining British stronghold and the French population becoming synchronously isolated.

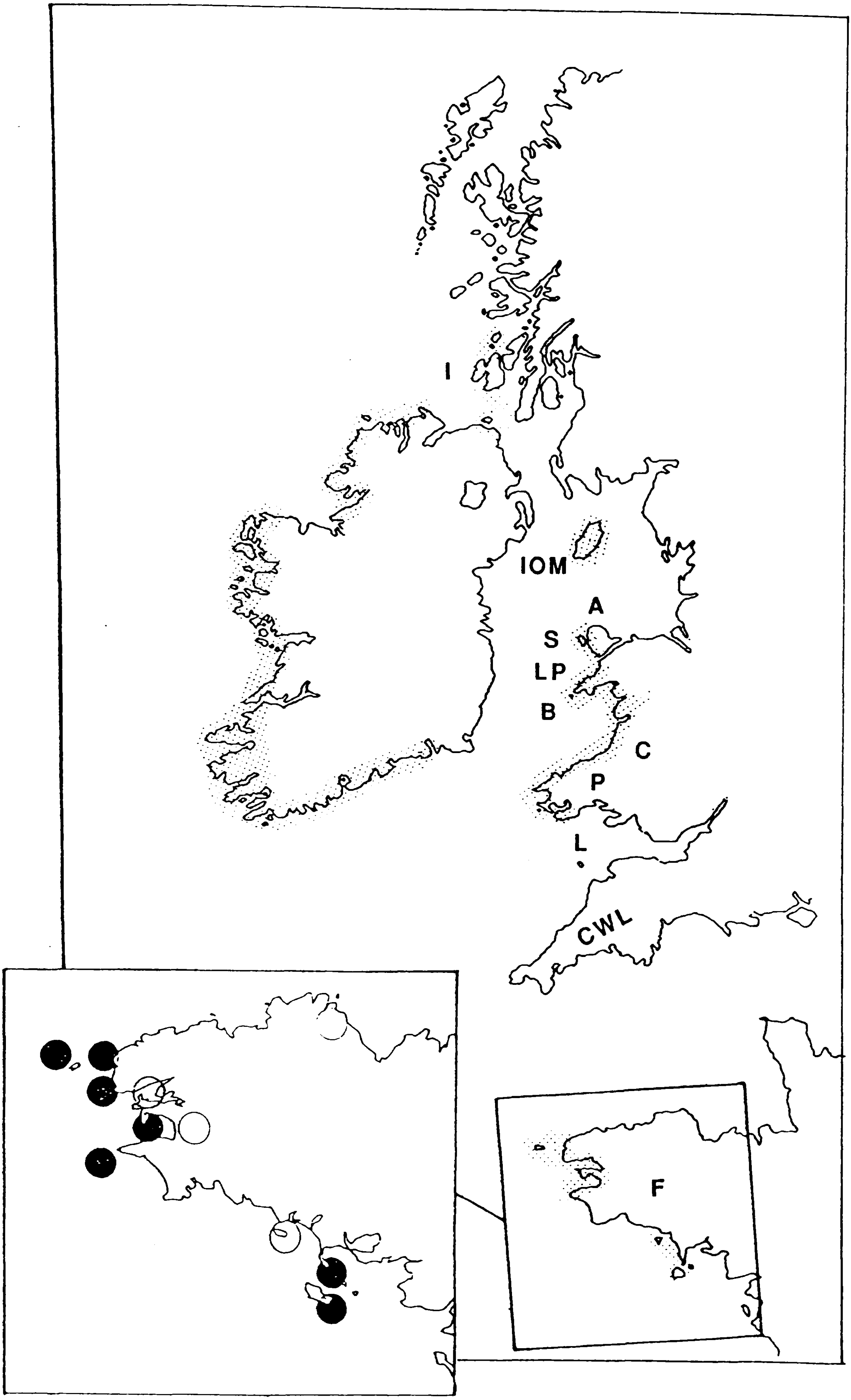
The Chough is the emblem of the Duchy of Cornwall. It is regarded by most Cornish people as their national bird, and it is a matter of considerable local pride embraced in Arthurian legend that it should some day return.

Figure 1.2

Distribution of the Chough in Britain, Ireland and Brittany, France (after Sharrock 1976, Guermeur and Monnat 1980, Lack 1986), showing also position of Cornwall, Lundy Island and Channel Islands. Stippling denotes breeding areas. Closed circles denote confirmed breeding and open circles denote possible breeding in Breton range

Key:

A	Anglesey
B	Bardsey Island
C	Ceredigion
CWL	Cornwall
F	France (Brittany)
I	Islay
IOM	Isle of Man
L	Lundy Island
LP	Lleyn peninsula
P	Pembrokeshire
S	South Stack


I
IOM
A
S
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CWL
F

This somewhat subjective desire has found expression within Cornwall for many years, and has recently been fuelled by national and European conservation interest in the species (*i.e.* EC Directive 1985) designed to afford protection within the greater European continent. Consequently, attention has been focussed on the status and biology of the species, notably in North Wales (see, *e.g.* Bullock 1980, Roberts 1985), western Scotland (see, *e.g.* Warnes 1982, 1983; Still 1989), Ireland (Cabot 1965, Bullock *et al.* 1983b) and the Isle of Man (see, *e.g.* Bullock & del-Nevo 1983, Bullock *et al.* 1983c). The southern limit of the range appeared to require similar effort in order to help guard against a continued northward retraction (see Bignal & Curtis 1989 for overview).

The study was bolstered by a timely opportunity to study wild Choughs in Cornwall when two individuals of unknown origin spent several months in the county during 1986 and early 1987 (see Appendix IV). These birds spent more than 90% of available time actively hunting for food, and helped concentrate the subsequent focus of the main study. By investigating the Chough's feeding ecology in West Wales (principally Pembrokeshire) and by relating these findings to the current situation in Cornwall, the study addresses the question "Can Cornwall support Choughs today?". It also examines factors which control the general distribution pattern of the species (see Sections 1.2 and 3). The ecological study is compared to a habitat assessment in which 185 1km squares in the Welsh and Cornish regions (2.2) were surveyed for quality of habitat. In order to best understand the reasons for the original decline, an historical survey was undertaken which included an analysis of changing land-use practices for 150 years since the 1840s within the coastal kilometre squares of the same two study regions (4.6).

1.2 OBJECTIVES AND RATIONALE OF THE STUDY

The specific objectives of the study are set out in Table 1.1.

Table 1.1 Specific objectives

1	Establish causes of decline of the Chough in England (principally Cornwall)
2	Investigate its feeding ecology in West Wales (principally Pembrokeshire)
3	Relate Welsh findings to current Cornish habitat state in order to establish current suitability for Choughs
4	Recommend management strategies to enable more effective conservation in existing Welsh range
5	Recommend management strategies to improve Cornish habitat

Because of the endangered status of the species, included within Annex I of the EEC Directive of Wild Birds, and particularly in Britain of the nominate race *Pyrrhocorax p. pyrrhocorax* (Schedule I status, Wildlife and Countryside Act 1981), considerable local Cornish and wider scientific interest in the project was evident from the beginning and lay behind its original conception.

In broader terms, beyond the question "Can Cornwall support wild Choughs?", advice is formulated on habitat management and other conservation strategies which is relevant to the further conservation of the Chough throughout its range. The Chough is increasingly seen as a 'flagship' species (Bignal & Curtis 1989), representative of quality habitat, *e.g.* species-rich habitat. In his Introduction to the 'International Workshop on the Conservation of the Chough in the EC', held in Pembrokeshire in 1988, Pienkowski (1989) described the Chough as being "generally associated with sensitive, threatened, semi-natural agricultural systems." He went on to say:

> "All areas supporting good Chough populations have forms of pastoral agriculture which are in sympathy with the natural environment. These areas tend to hold many other features of nature conservation interest, including their plant communities" and
>
> "The Chough an be regarded as an indicator of these diverse environments."

Some of the advantages that might ensue from a viable population of Choughs being established in Cornwall are given in Table 1.2.

Table 1.2 Potential benefits accruing from successful re-establishment of the Chough in Cornwall

1 Increased protection of existing population
2 Extension of existing range
3 Reduced isolation of French sub-population
4 Information resulting in the better protection/management of western maritime cliffs
5 Benefits to cultural and economic interests in Cornwall

To sum up, the present British population would be strengthened and the decline reversed in a visible way; the Breton population would be less isolated, and considerable benefits might accrue to local Cornish interests. More importantly, perhaps, in respect of (4) in Table 1.2, because the Chough is a key species at the top of the food chain for the western maritime cliffs, only superseded by the Peregrine falcon, the maritime cliff environment might be better understood, thus enabling more positive management of a biotope, recognised, in national conservation circles, as a priority (Nature Conservancy Council 1989). One way of illustrating this is by reference to the now extinct but formerly closely sympatric Large blue butterfly *Maculinea arion*: the decline of the Large blue occurred at much the same time as that of the Chough (Thomas 1977). The Chough would have certainly predated upon it; and its disappearance would have been a further check to prospects of Chough survival. An implementation of better understood Chough ecology would have helped protect the Large blue's habitat to both species' mutual benefits.

The Chough has declined markedly across southern Britain in historic times (Bullock *et al*. 1983a, Owen 1985). From these surveys, no single cause seems pivotal (Rolfe 1966), but changes (mainly reductions) in sheep-farming and direct persecution (egg-collecting, shooting and trapping) are presented as being crucial (see also Owen 1989). Competition from other species, notably the Jackdaw was commonly cited as the main cause and is still given some credence today. Other changing agricultural practices, as they affected the Chough's habitat, will also have had an effect, either independently or in concert; the decline is discussed in Chapter 3.

It was decided to assess the quality of ex-Chough habitat in the most recently abandoned area (*i.e.* Cornwall) by examining the Chough's ecological requirements in the nearest occupied region (*i.e.* West Wales). These findings are compared to the results of equivalent background work in Cornwall. It was hoped that from these dual inquiries it would be possible to make recommendations towards an improved ecological management of both regions: specifically, to (i) help preserve the population in West Wales; and (ii) improve the Cornish habitat with a view to possible re-establishment.

1.3 A RESUME OF THE BIOLOGY OF THE STUDY SPECIES IN BRITAIN

1.3.1 DESCRIPTION

The Chough is unique among the British Corvidae in being a specialised, largely insectivorous bird, easy to distinguish at close quarters from the 'typical crows' of the genus *Corvus* (Goodwin 1986). It is a medium-sized crow, measuring 350-400mm long and weighing approximately 250-300g.

Table 1.3 Weights of 15 captive Choughs; sexual status determined by laparoscopy

Sex	Mean wt (g)	SD (g)	N
Female	253.5	37.39	8
Male	285.4	39.52	7

t-value = 1.6, N.S.

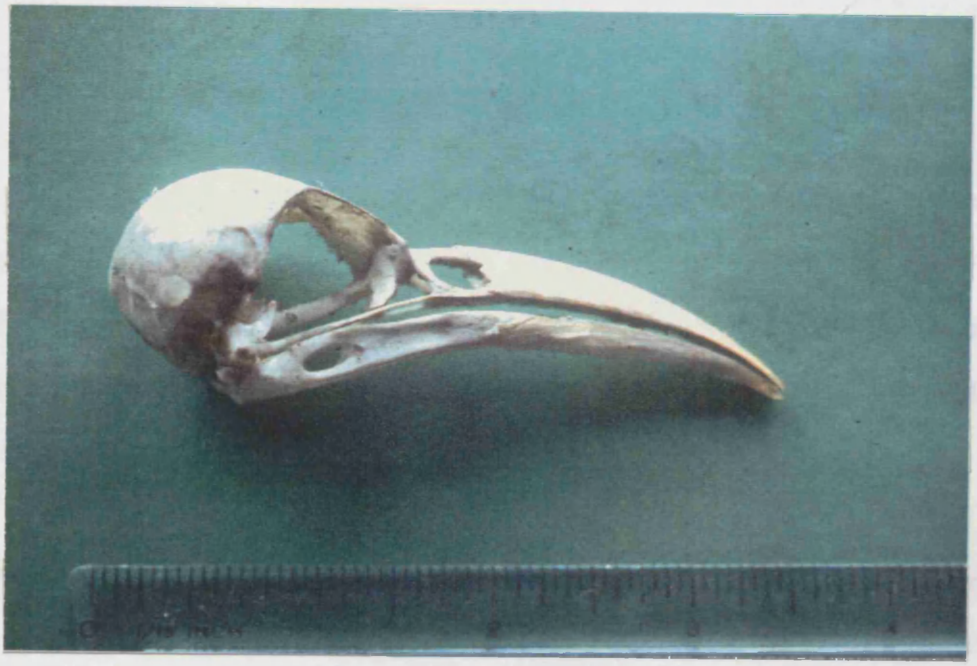
Males are often heavier than females but morphological sexual dimorphism is not marked and no significant difference was found in the weights of a small captive sample (Table 1.3). The bill length of 5 sub-adult females ranged from 480mm to 550mm, that of the solitary male available was 560mm; so it is possible that there is a slight overall size difference as well but sample sizes will need to be increased before it is possible to be didactic about this. The overall black plumage ("its feathers are of a much richer velvet black than those of other crows" said Borlase in 1758) has a distinctive metallic sheen contrasting with the vermilion 50mm decurved bill and legs of the same colour. Like Goodwin (1986), I have also recognised in the structure of its bill (Figure 1.3) and predominant mode of feeding (pecking and shallow probing of the substrate, Figure 1.4) a resemblance to the Hoopoe; indeed, the Chough was named by Linnaeus as *Upupa pyrrhocorax* ('Fire-raven hoopoe'), and its feeding behaviour and bill structure argue against a closely competitive relationship with the Jackdaw (Goodwin 1986; Section 3.3.5) or, indeed, any other Eurasian crow, which have heavy duty bills with a tearing edge, suitable for a generalist predator-scavenger (Waite 1984). Decurvature of the bill, unique in British corvids, argues strongly for specialised feeding habits (*ibid.*, Davidson *et al.* 1986). The latter authors, in a paper which may be extended to other species, discuss decurvature in the Curlew's bill structure, and conclude, *contra* Owens (1984), insofar as it aids manoeuvrability beneath ground, that it evolved as a means for gentle probing along precise but complex routes. Other species, including the Hoopoe, wood-hoopoes and treecreepers are introduced in defence of this conclusion, and the Chough might well have been. Such bill structure is also helpful in foraging for insects in grassland, a curved bill also aids the extraction of worms (whole) and provides for the longest effective bill commensurate with shorter leg length, necessary to counteract the effect of buffeting in windy conditions (*ibid.*; and see Section 6.4). To a cliff or montane species, especially one which lives on a windswept coastline, long legs would presumably not be selected for.

Figure 1.3

Skull of Red-billed chough; from a Peregrine kill at Strumble, Pembrokeshire

Figure 1.4

Choughs feeding (in captivity)


1/16 INCH
2
3
4

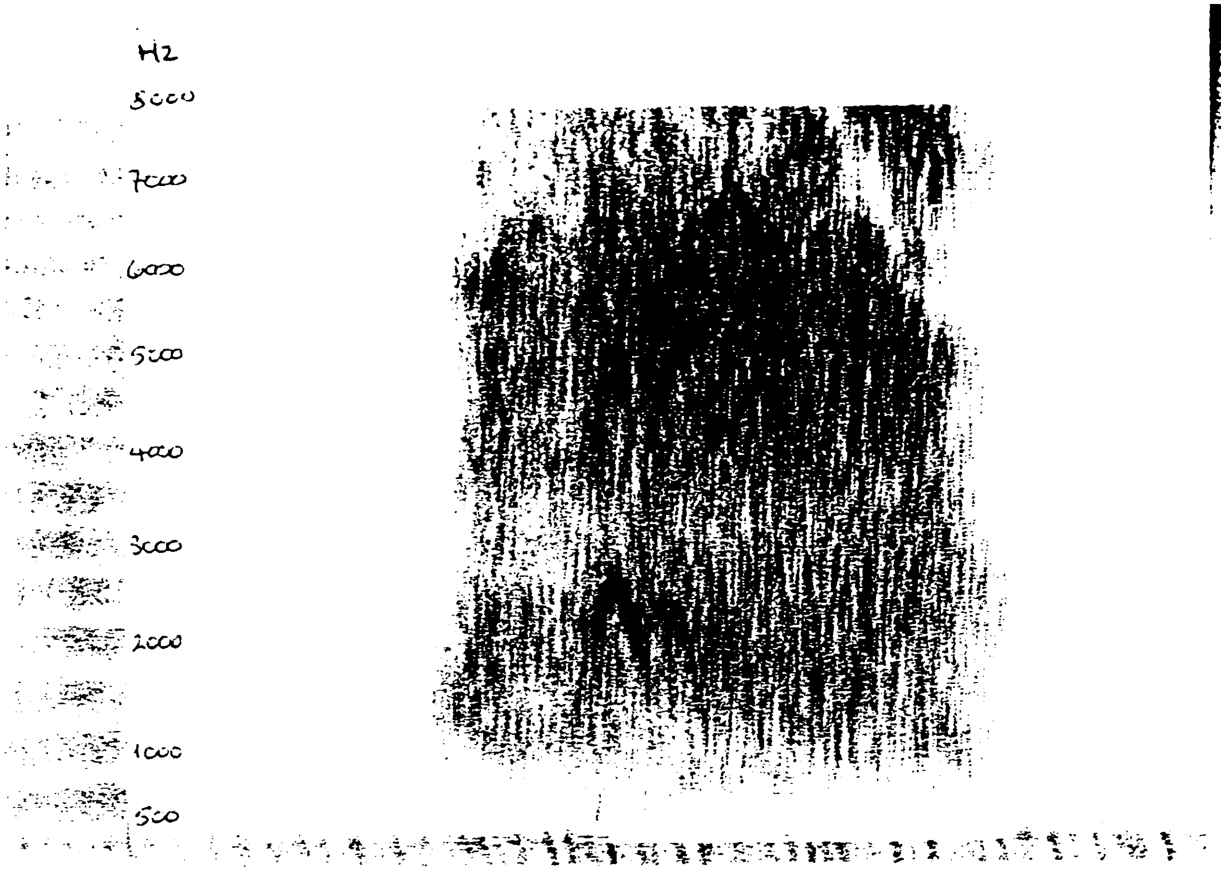
The Chough has the virtuoso flying skill expected of a bird which habituates such storm-tossed cliffs and which nests in crevices and sea caves inaccessible to most (if not all) other sympatric terrestrial vertebrates. The Chough hunts for its largely invertebrate diet, supplemented in the autumn with cereal grain (see Chapter 5), on these cliffs and adjoining low grade agricultural land.

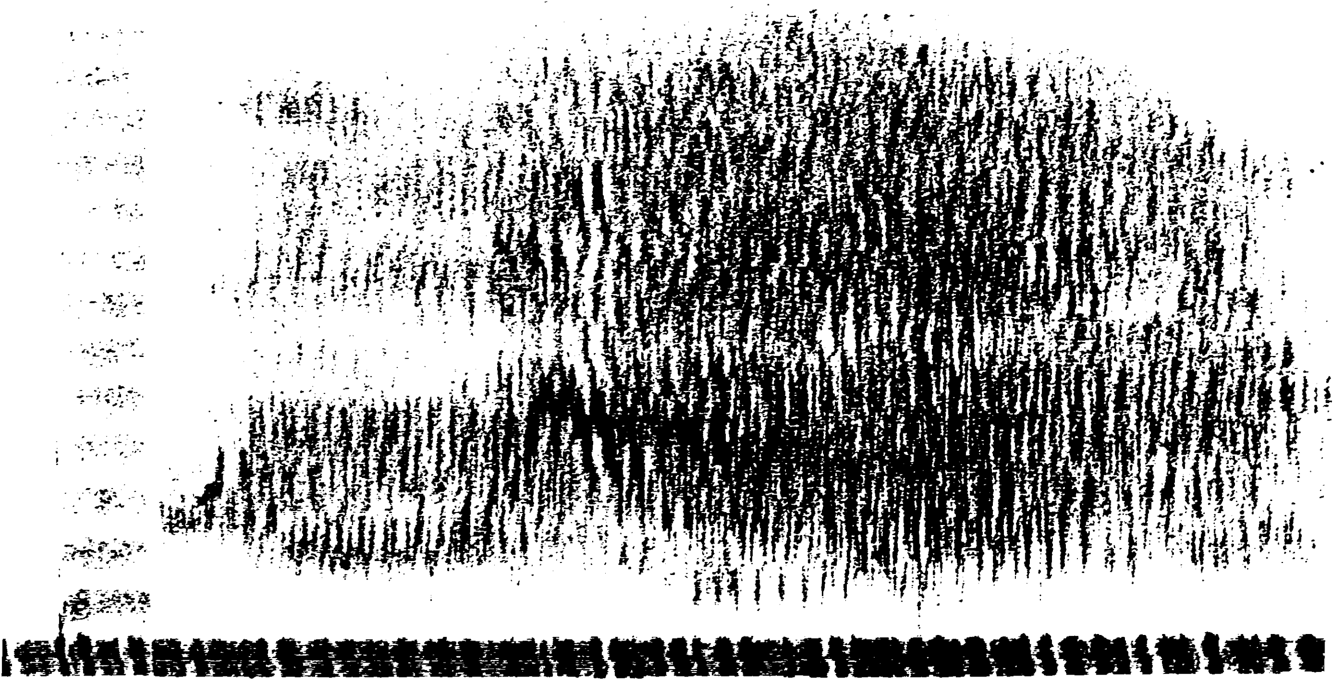
The most frequently heard vocalisation is an onomatopoeic '*keeah*' or '*t'cheea*' (Goodwin 1986; see Figure 1.5 and Section 2.5.1). Earlier authors, notably Whittaker (1947) and Williamson (1959), and many since, have described it as '*kee-ah*' or '*ch(w)ee-ow*'. The pronunciation of Chough has likely been anglicized to 'chuff' though it is still pronounced 'chaw' or 'chow' in parts of western Cornwall (Beckerlegge 1972, pers. obs.). Observations in captivity and the wild suggests to me that there might be some sexual dimorphism in the call (Figure 1.5) but this requires further work.

Peak egg production in Choughs is during April (Holyoak 1967) through to mid-May (Goodwin 1986). Choughs usually lay 3-4 eggs (range 1-6) (Bullock *et al*. 1983a); Goodwin (1986) gives 3-5, exceptionally 2,6 or 7. The female alone incubates, during which time she is fed by the male. It has not been conclusively established whether or not incubation begins with the laying of the first egg; in all British corvids, with the possible exception of the Chough, hatching is asynchronous (Holyoak 1967). It is therefore possible that, in the Chough, incubation (17-18 days) begins

Figure 1.5

Sound spectograph of Chough calls. A known true captive pair (sexed by laparoscopy) calling in unison. The provisional graphs support the idea that the sexes can be differentiated by their voice. Top: the call pattern in real time, .63 seconds duration; indication of point at which second bird call commences, note disjunction of pattern up to and above 3,000 Hz. Bottom: the same call at half speed. Density of pattern represents volume.


Hz
8000
7000
6000
5000
4000
3000
2000
1000
500



when the first egg is laid. Guichard (1962) and Witherby *et al.* (1943) concur, but Ryves (1948), who had considerable knowledge of the species in Cornwall, asserts that incubation does not commence until the last egg is laid; maybe, as suggested by Goodwin (1986), there is individual variation.

Young Choughs lack the striking red colouration of bill and legs when they leave the nest, usually in late June or early July, and at that time quite closely resemble their only congener the Alpine Chough *P. graculus*. The red colouration is soon obtained, and by August or September they resemble their parents. Both parents would seem to care for the young post-fledging (Cowdy 1962, pers. obs.) despite the statements of some earlier authors, *e.g.* Schifferli & Lang (1941). There is a lack of data on wild Chough mortality (Holyoak 1971a); *ca.*50% of fledged Choughs on Islay survived for at least two years (Bignal *et al.* 1987a). A longevity of at least 20 years is suggested by the documented histories of the last two Cornish birds: the last confirmed breeding was in 1947 (Penhallurick 1978) and it is believed that these birds or, as is more likely, their offspring, survived until 1967 and 1973. It cannot, of course, be proved that these birds were the same two; the longest proven longevity of a wild Chough is a Bardsey ringed bird of at least 17 years (Roberts 1985). Captive longevity is predictably greater (3.4.6b).

1.3.2 DISTRIBUTION, STATUS AND HABITAT

The present western bias of the Chough has already been noted (and see Figure 1.2). It has a linear distribution and is confined mainly to remote yet grazed stretches of cliff-dominated coastline (Sharrock 1976, Lack 1986); these conditions are best met with on off-shore islands which are large enough to support farming (7.3.2).

The species breeds in isolation and not in colonies, contrary to what is often stated. In Wales and Britany, this has led to overestimates of population size: observed flocks, especialy in spring, are assumed to be breeding pairs rather than surviving immatures and non-breeding adults in unknown proportions (Guermeur & Monnat 1980). In historic times, the distribution was wider (see Chapter 3) although, perhaps, always patchy (Monaghan 1989), with inland components and localities in Scotland as extreme as Cape Wrath at the north and St. Abb's Head in the east (Baxter & Rintoul 1953). Inland breeding sites are notable in Ireland (mainly Co. Kerry): <17km from the coast (Ussher & Warren 1900) and 19km (Bullock *et al.* 1983b). The latter authors showed that these sites were still being used in 1985, similarly for the locations in North Wales. The Welsh sites were situated in coastal quarries <2km inland (n=9); Snowdonia, 8-18km from the coast (n=33); with a further isolated three, as far as 28km inland. Bullock *et al.* (1983a) found that 14% of nest sites in Britain and Ireland were inland: mainly in quarries, mine shafts and derelict or little-used buildings. In Wales (due to the Snowdonia population) and Scotland (predominantly Islay) the figure is just over 30%. Irish and Manx figures of *ca*. 8% but of a far greater base (~~see~~ ca. 700 prs and 55 prs respectively ~~Section~~ [illegible]) account for the lower overall percentage. On Islay, inland nest sites in man-made sites have increased from zero in the early 1970s to 25-30% (Bignal *et al*. 1987, 1989) possibly due to an increase in the population consequent upon more effective protection and a spill-over from preferred natural sites. If so, it not only suggests that, prehistorically, Choughs might have been found wherever there was sufficient good year-round feeding habitat and nest sites for breeding birds, and support ground also for non-breeders (see Bignal *et al*. 1989), but also that a similar expansion within the usual dispersal range is possible.

Classically, though, in Britain, Choughs associate with maritime cliffs. Ratcliffe (1980), in describing the cliff-bound seaboard of SW England for the Chough's only real predator, the Peregrine (3.4.5), also conveyed an accurate impression of Chough habitat:

> "...in this strong oceanic climate, the soils tend to be relatively acidic and infertile. The farms have less arable land and a prevalence of permanent grassland. There was once a large extent of unenclosed rough pasture and heathland with heather, bracken and gorse at the back of many stretches of cliff, but the war on unproductive land has spread here; and many such areas have been 'reclaimed'. The combination of plough, fertiliser, pesticides and seed-drill have increasingly brought the enclosed land right to the cliff edge, and much of it is now arable. Some areas ... remain, but

> here again myxomatosis and the demise of the rabbit have often been followed by development of dense scrub, especially with gorse and brambles."

In Section 3.4.6e, gross changes in land use as they might have affected Choughs are discussed, and in Chapter 4 an attempt is made to assess the change.

The changes in Chough status have received more attention. Bullock *et al.* (1983a), updating and reanalysing an earlier census (Rolfe 1966), showed little change in numbers (2635-2776 individuals, of which 31-32% were non-breeding individuals) or in distribution (*cf.* Sharrock 1976). The population in Wales in 1982 (the most recent full census) was estimated as 139-142 pairs + >100 non-breeders; a "probable increase" since 1963 (Bullock *et al.* 1985). The two strongholds for the Chough in Wales are Caenarvonshire in the north and Pembrokeshire in the south, which support 72% of the Welsh breeding population (*ibid.*). Donovan (1972), midway between the two major censuses, estimated 46 pairs; Rolfe possibly underestimated at 33-36 pairs. The inland population of Snowdonia is about 25 pairs, half that given by Lovegrove (1987) although he might have been including some coastal pairs. A recent census in Scotland revealed 105 breeding pairs, 90% of which were on Islay (Monaghan *et al.* 1989). The population on the Isle of Man represents about 6% of the total for Britain and Ireland: 49-60 pairs (Bullock *et al.* 1983c), approximately the same as for Pembrokeshire.

2 METHODS

2.1 INTRODUCTION

Islands, where comparatively high numbers of Choughs are concentrated in discrete areas, provide good opportunities and facilities for ecological study (*e.g.* Bullock 1980, Bullock & del-Nevo 1983, Roberts 1985, Warnes 1982, Still 1989, and McKay in prep.) but the ecology of mainland Choughs has been little studied (*cf.* Owen 1985). Objective research on the species has occurred principally in North Wales and on Islay. [illegible] Of the above studies, Ian Bullock pioneered work into Chough behavioral ecology on Anglesey and the Isle of Man, followed notably by Warnes on Islay, and Roberts on Bardsey. The Islay effort is continuing (*e.g.* Monaghan *et al.* (1989), Still (1989), and McKay (in prep.). Within Europe generally there is growing interest (see Bignal & Curtis 1989). This body of work has greatly increased knowledge whilst at the same time revealing paradoxes and gaps.

Published work on the Chough in West Wales relies largely on the censuses of Donovan (1973) and Roderick (1978). The Nature Conservancy Council (NCC) in Dyfed-Powys, Wales was concerned about the status of the species (see, *e.g.* Gamble 1984, Gamble & Haycock 1988), therefore the Welsh and Cornish/English interests were integrated into the research objective explained in Section 1.2.

The methods employed in this study are essentially twofold and of a comparative nature:

(1) broad comparison of Welsh areas within current Chough range, and Cornwall currently outwith Chough range, followed by a more sensitive

comparison of resources used by Choughs within the Welsh areas, again related to Cornwall; and

(2) comparison of past land-use regimes with present day regimes within and between Wales and Cornwall. This duality of habitat assessment required the selection of 2 levels of study areas: (i) large scale uniform selection of 1km squares including both used and unused habitats, inland and coastal (2.2); and (ii) smaller observational study areas within these (2.3).

Regarding bird observation, unlike the island communities referred to above, *i.e.* South Stack (Anglesey), Bardsey, Islay and the Calf of Man, the Choughs in Dyfed are scattered thinly along an extensive mainland coastline. Practical and technical problems beset the study of low density populations, especially when distributed through 5 separate study areas over more than 100km of coastline (2.5.1). The Cornwall element was located *ca*.120km across the Bristol Channel (a road journey of >480km). The Cornish effort was spread over 4 sub-areas (all historically important for Choughs) separated along >230km of coast (2.3). A study circuit of all study sites involved a round trip of *ca*.1500km every 6-8 weeks.

2.2 BACKGROUND HABITAT ASSESSMENT

Habitats in Wales and Cornwall were sampled in order to assess broad features of land type. Bunce & Shaw (1973) have stressed the importance of objectivity and standardisation in ecological sampling and surveying techniques. To maximize the benefits of this study, it was designed to be compatible with a similar study on Islay (Bignal *et al.* 1988, Curtis *et al.* 1989), but comparison is beyond the scope of the present study. The full methodology is given in Section 4.2.1. Six areas (3 each in Wales and Cornwall; see Appendix II and Figure 2.1), subdivided on the Ordnance Survey (OS) km square grid matrix (Figures 2.2 - 2.5), were used for the initial assessment. These were selected to provide fundamental habitat data within principal Chough and ex-Chough regions. A total of 184 1km^2 (94 in Wales and 90 in Cornwall) were selected as shown in Table 2.1.

Within the separate study blocks, the sample 1km^2 were surveyed 'field-by-field' on 1:10,000 scale maps, and annotated (see Figure 4.1), as recommended within the Institute of Terrestrial Ecology project, *Changes in the Rural Environment*, for natural, semi-natural and agricultural features. Vegetation cover types plus all species with a frequency of >19% within a minimum mappable unit of 1/25ha and a minimum mappable length of 20m (1/50km) were recorded. Descriptive information such as agricultural usage and vegetation heights were also recorded because of their effect on the presence and availability of food resources. The environmental data were transformed into raster as described in Section 4.2.1.

Figure 2.1

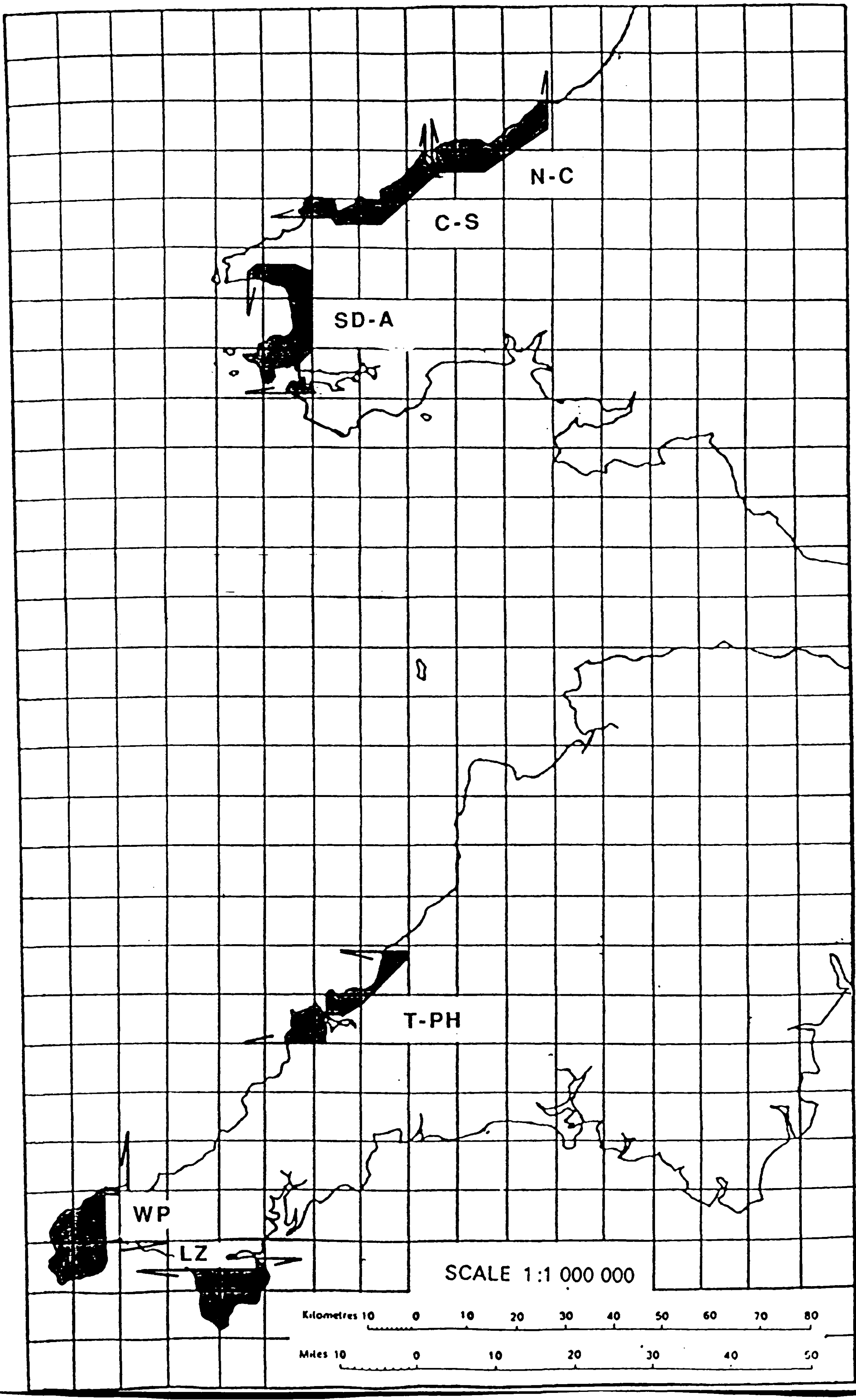
Habitat assessment regions in Wales and Cornwall

Key (Wales):

N-C	Newquay (Ceredigion) to Cardigan
C-S	Cardigan to Strumble Head
SD-A	St Davids to Angle

Key (Cornwall):

T-PH	Tintagel to Park Head (North Cornwall)
WP	West Penwith
LZ	The Lizard


N-C
C-S
SD-A
T-PH
WP
LZ
SCALE 1:1 000 000
Kilometres 10 0 10 20 30 40 50 60 70 80
Miles 10 0 10 20 30 40 50

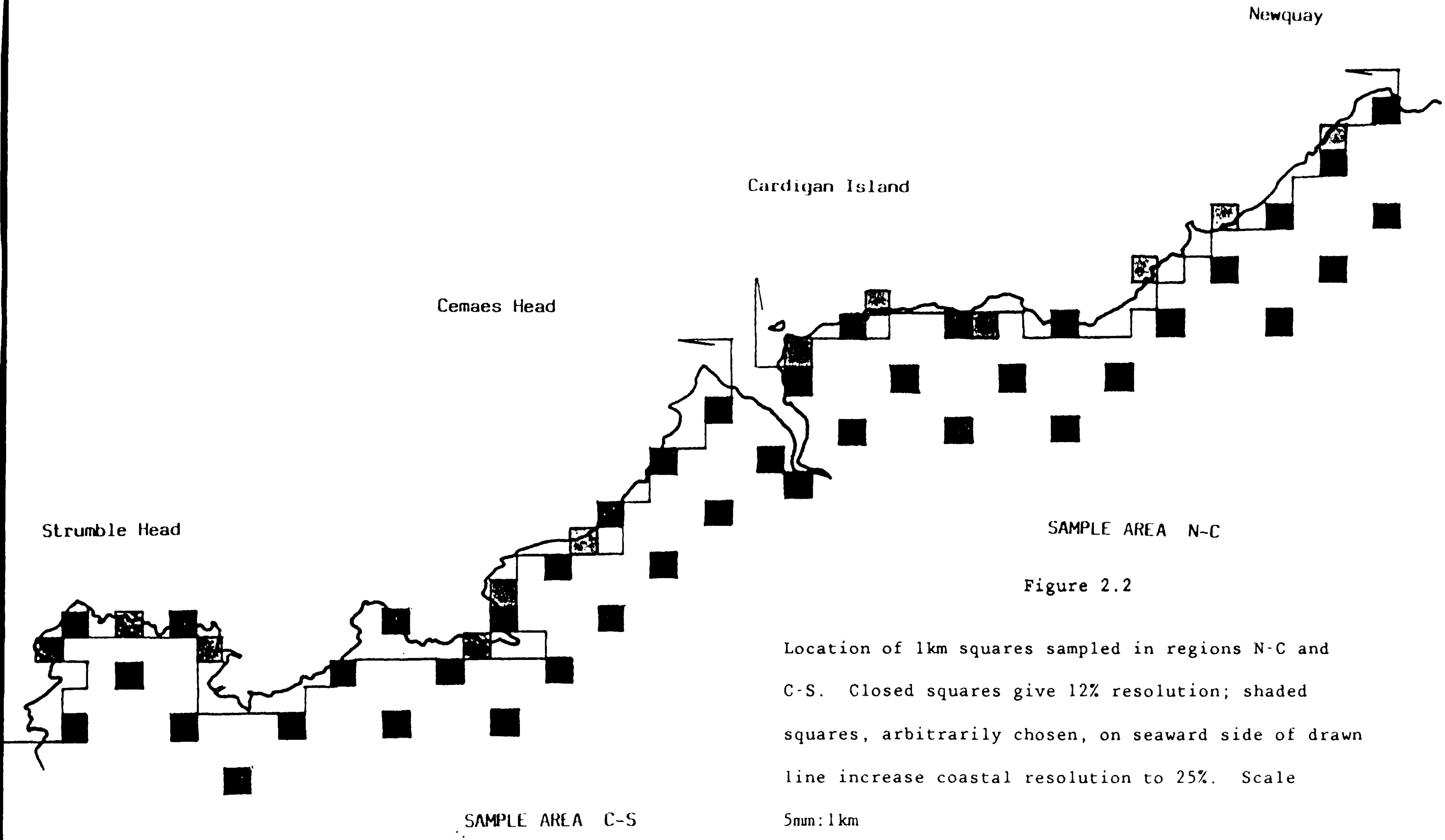
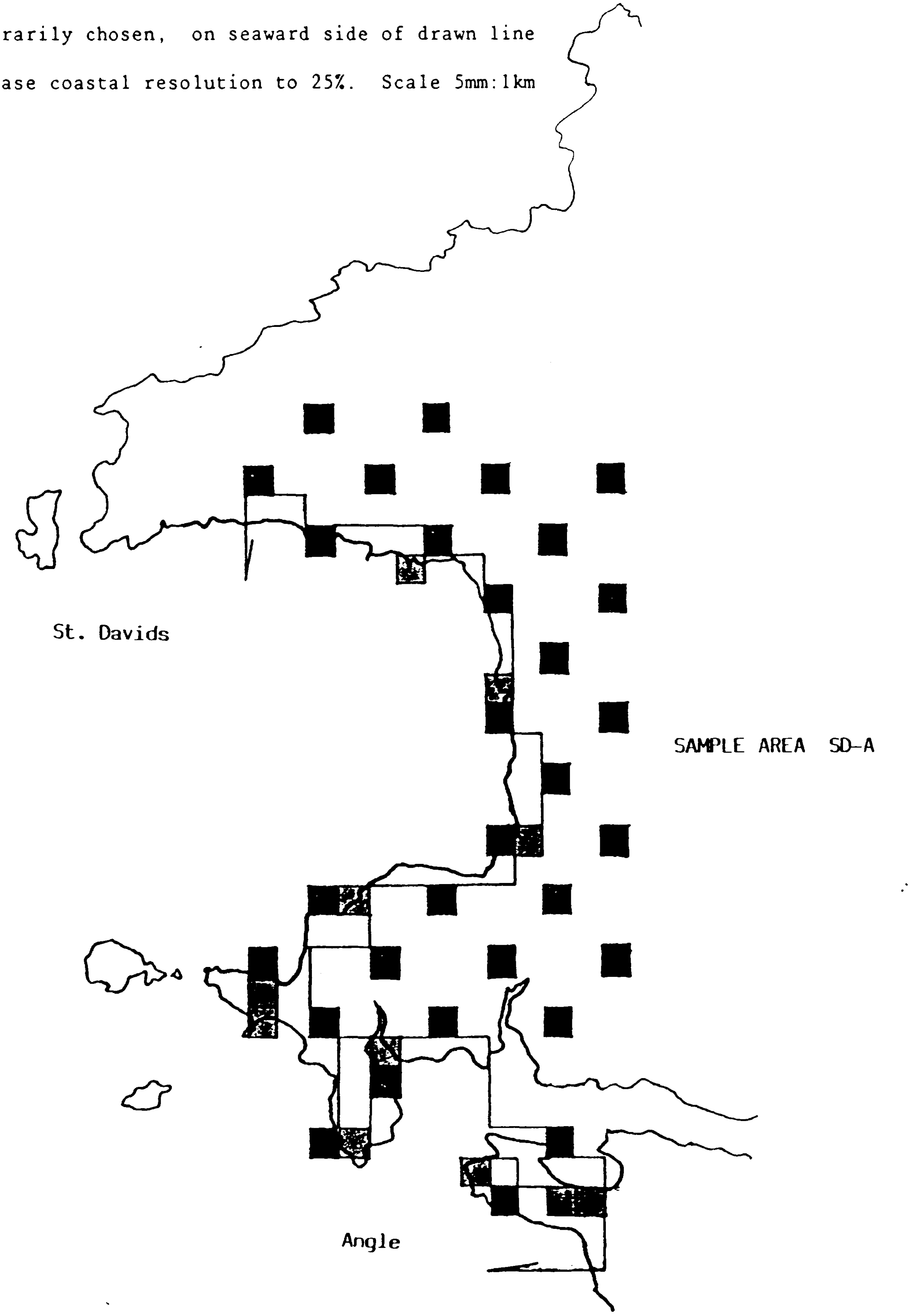

Newquay
Cardigan Island
Cemaes Head
Strumble Head
SAMPLE AREA N-C
SAMPLE AREA C-S

Figure 2.2

Location of 1km squares sampled in regions N-C and C-S. Closed squares give 12% resolution; shaded squares, arbitrarily chosen, on seaward side of drawn line increase coastal resolution to 25%. Scale 5mm:1km

Figure 2.3

Location of 1km squares sampled in region SD-A. Closed squares give 12% resolution; shaded squares, arbitrarily chosen, on seaward side of drawn line increase coastal resolution to 25%. Scale 5mm:1km


St. Davids
SAMPLE AREA SD-A
Angle

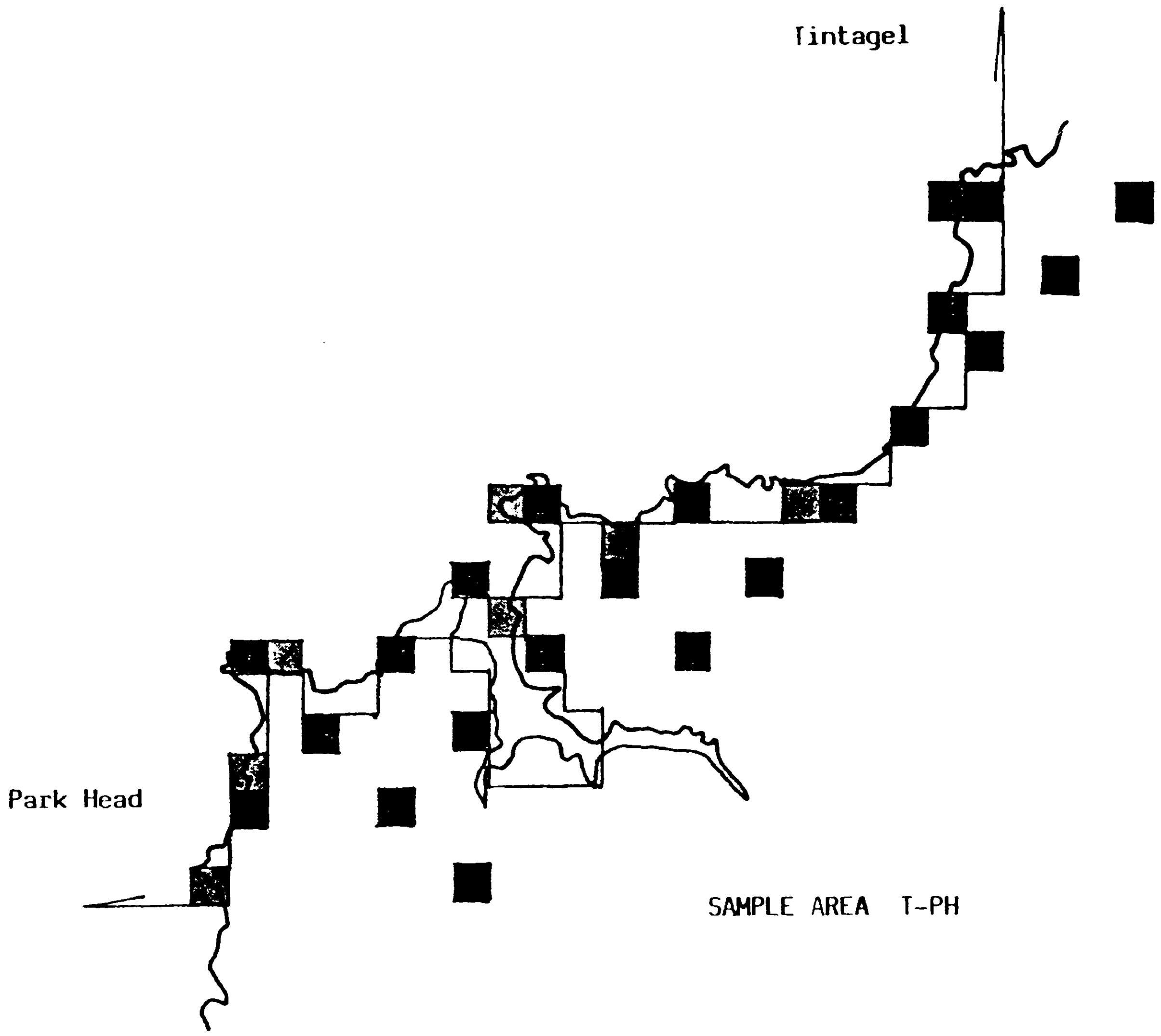

Tintagel
Park Head
SAMPLE AREA T-PH

Figure 2.4

Location of 1km squares sampled in region T-PH. Closed squares give 12% resolution; shaded squares, arbitrarily chosen, on seaward side of drawn line increase coastal resolution to 25%. Scale 5mm:1km

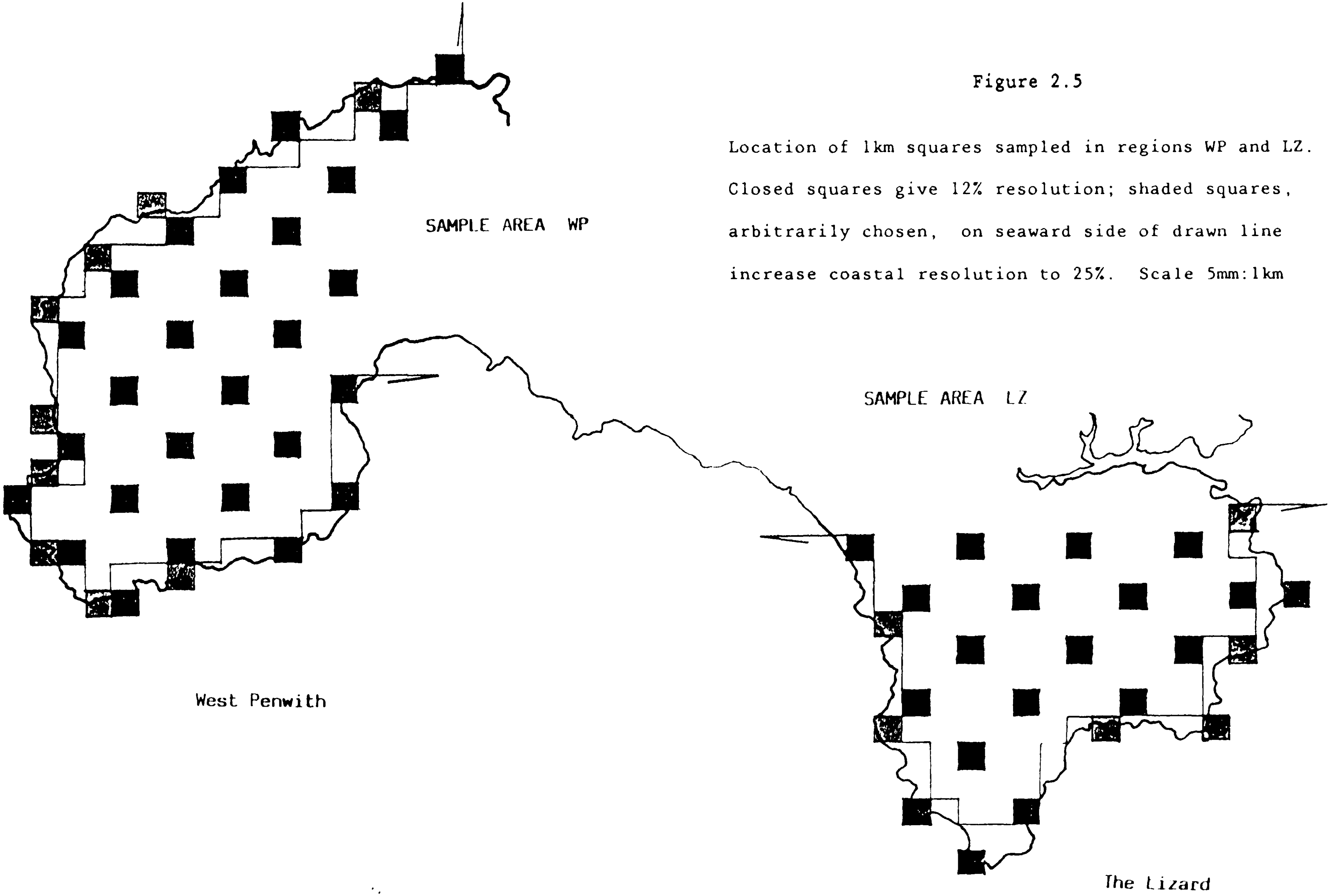

SAMPLE AREA WP
SAMPLE AREA LZ
West Penwith
The Lizard

Figure 2.5

Location of 1km squares sampled in regions WP and LZ. Closed squares give 12% resolution; shaded squares, arbitrarily chosen, on seaward side of drawn line increase coastal resolution to 25%. Scale 5mm:1km

Table 2.1 Kilometre squares surveyed in habitat assessment. The 12% background sample was increased incrementally on coastal squares to give *ca.*25% resolution

	Kilometre Squares		
Study Block	Grid Sample *ca.*12%	Additional Coastal *ca.*25%	Total
Newquay-Cardigan	18	6	24
Cemaes-Strumble	23	6	29
St Davids-Angle	31	10	41
Total Wales	72	22	94
Tintagel-Park Head	20	9	29
West Penwith	27	9	36
The Lizard	18	7	25
Total Cornwall	65	25	90
GRAND TOTAL	137	47	184

Each 1km^2 was effectively mapped 3 times (see Figure 4.1), yielding 7500 packets of descriptive information. Additional physiographical details were recorded, *e.g.* topography was assessed for cliff height and natural nest sites but since this can be safely assumed not to have changed significantly over time it is excluded from the present analysis. Similarly, woodland and scrub were measured but these are negative features since, as with long vegetation they prevent access to invertebrate food resources. The scrubbing over of headlands and clifftops consequent upon a reduction in grazing was suggested as a contributory factor in the decline 20 years ago (Darke 1971; see Chapter 4). Whittaker (1947) was the first to record a link between grazing and Choughs, but it was not to be demonstrated for a further 30 years (Bullock 1980, Bullock & del-Nevo 1983).

2.3 THE OBSERVATIONAL STUDY AREAS

2.3.1 INTRODUCTION AND SELECTION CRITERIA

Selection of the study areas within the regionalised blocks was based principally on Chough distribution taken from, in Wales, NCC unpublished data, information from local naturalists, and notes made during the mapping survey described above; and, in Cornwall, knowledge of ex-distribution acquired from the literature (3.1 *et seq.*). Supplementary information may be gleaned from old place names, such as 'Chough's Ogo' (=Chough's cave) on the Lizard, Cornwall (see Figure 2.13). Boundaries of study areas were determined by bird exploitation (see Chapter 6 and Appendix VIII) established during pursuit periods (2.5.2) and surrounding visible area.

The selection criteria were:

Wales. Topography in key Chough regions to have comparable physiography to Cornwall. The study sites were chosen to provide a representative selection of the habitats exploited by Choughs in West Wales excluding the Old Red Sandstone region near St. Anne's Head in the far south. This area was not selected because (i) it has no physical equivalent elsewhere in the region or in Cornwall, and (ii) it is already the subject of a Chough-related inquiry (Gamble & Haycock 1988). For similar reasons and access problems, the island reserves of Skomer and Ramsey also received less attention. All these areas, however, were visited on one or more occasions, and their wardens provided valuable data. The two islands were, however, visited for study periods of several days (see Appendices V and VI). All Welsh study areas, with the exception of the northerly section (Mwnt-Cemaes; see Section 2.3.2), were linked and traversed by the Pembrokeshire Coast Path, which is administered by the Pembrokeshire Coast National Park (PCNP), and is largely of SSSI (Site of Special

Scientific Interest) status.

Cornwall. Ex-Chough areas with (i) a history of recent occurrence (*e.g.* North Cornwall); (ii) a discrete area with on-going sympathetic management and scientifically important (*e.g.* the Lizard); and (iii) strategic importance (*e.g.* West Penwith/Lands End), *i.e.* an area of great historic importance, compact with an extended coastline and forming a continuum between (i) and (ii). See Table 7.3 for detailed rationale.

2.3.2 THE WELSH STUDY AREAS

STUDY AREA W1: MWNT-CEMAES (Figure 2.6a-c, and see Appendix VIII). The northernmost area ($4^{o}38$-46'W, $51^{o}06$-08'N), effectively bisected into two sub-areas by the Teifi estuary and the town of Cardigan. The Cemaes section (*ca*.145ha) was located to the west in Pembrokeshire and the Mwnt section (*ca*.85ha) to the north-east of the Teifi in Ceredigion. Long gently declining vegetated slopes and cliffs of Ordovician rocks (0-100m), bounded to landward by a variable maritime mosaic of occasionally grazed semi-natural heath or scrub grassland, giving way to low-intensity pastoral-based agriculture of essentially upland character. In 1988 (and possibly 1989), one pair of Choughs nested unsuccessfully at Mwnt. At Cemaes, one of two pairs nested successfully in 1988 (the unsuccessful pair being possibly too disturbed by a nearby Peregrine eyrie); in 1989, both pairs were successful, the neighbours at the Peregrine site moving farther away around a headland.

Much of the ownership is controlled by conservation interests (National Trust (NT) and Dyfed Wildlife Trust) with guidance from the NCC. Both

Figure 2.6a

Study area W1. Dotted lines show eastern Mwnt section (see Figure 2.8b) and western Cemaes section (see Figure 2.8c) separated by Teifi estuary and the town of Cardigan

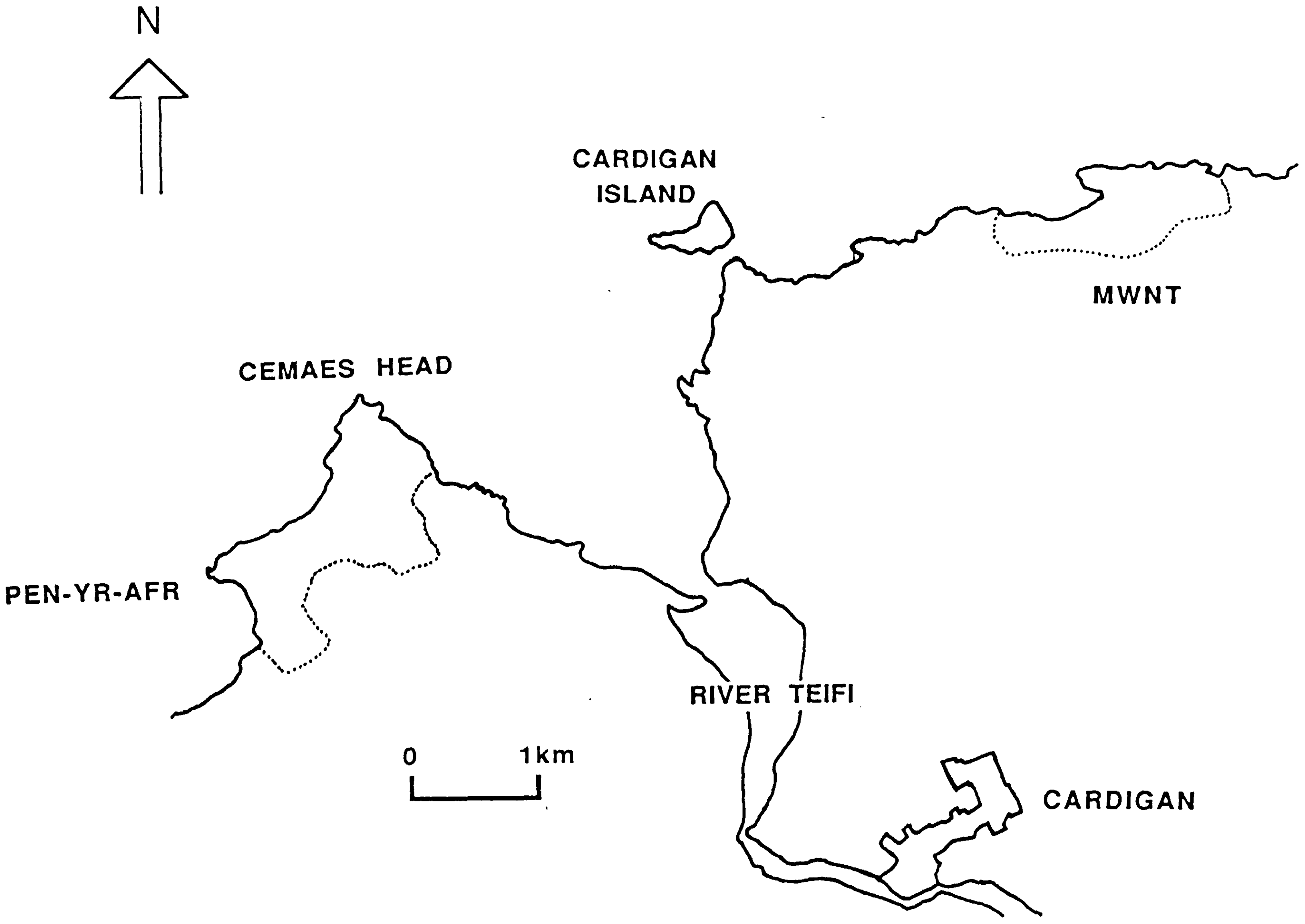
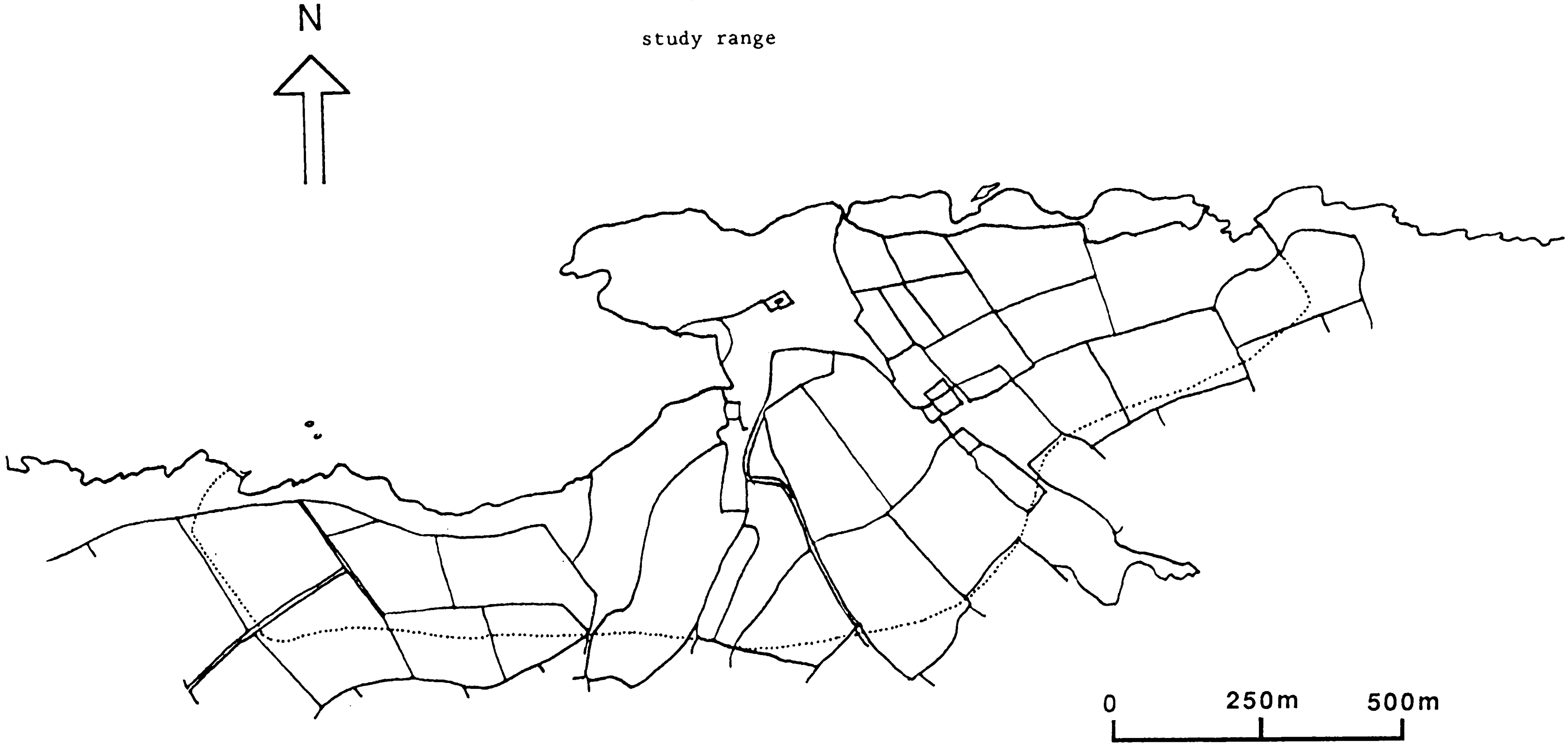

N
CARDIGAN ISLAND
MWNT
CEMAES HEAD
PEN-YR-AFR
RIVER TEIFI
0
1km
CARDIGAN

Figure 2.6b

Study area W1: Mwnt section. Dotted line delimits study range


N
0
250m
500m

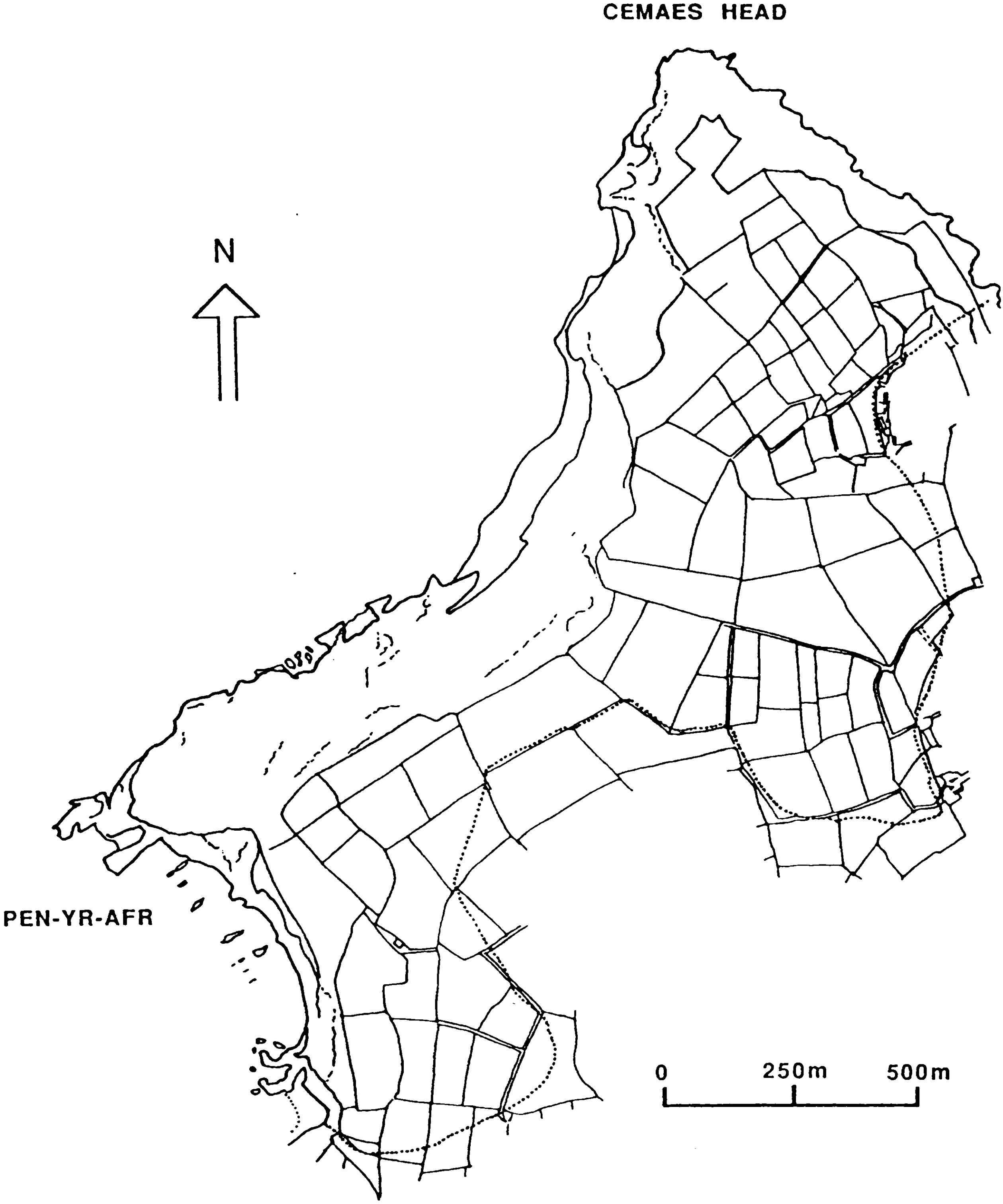

CEMAES HEAD
N
PEN-YR-AFR
0
250m
500m

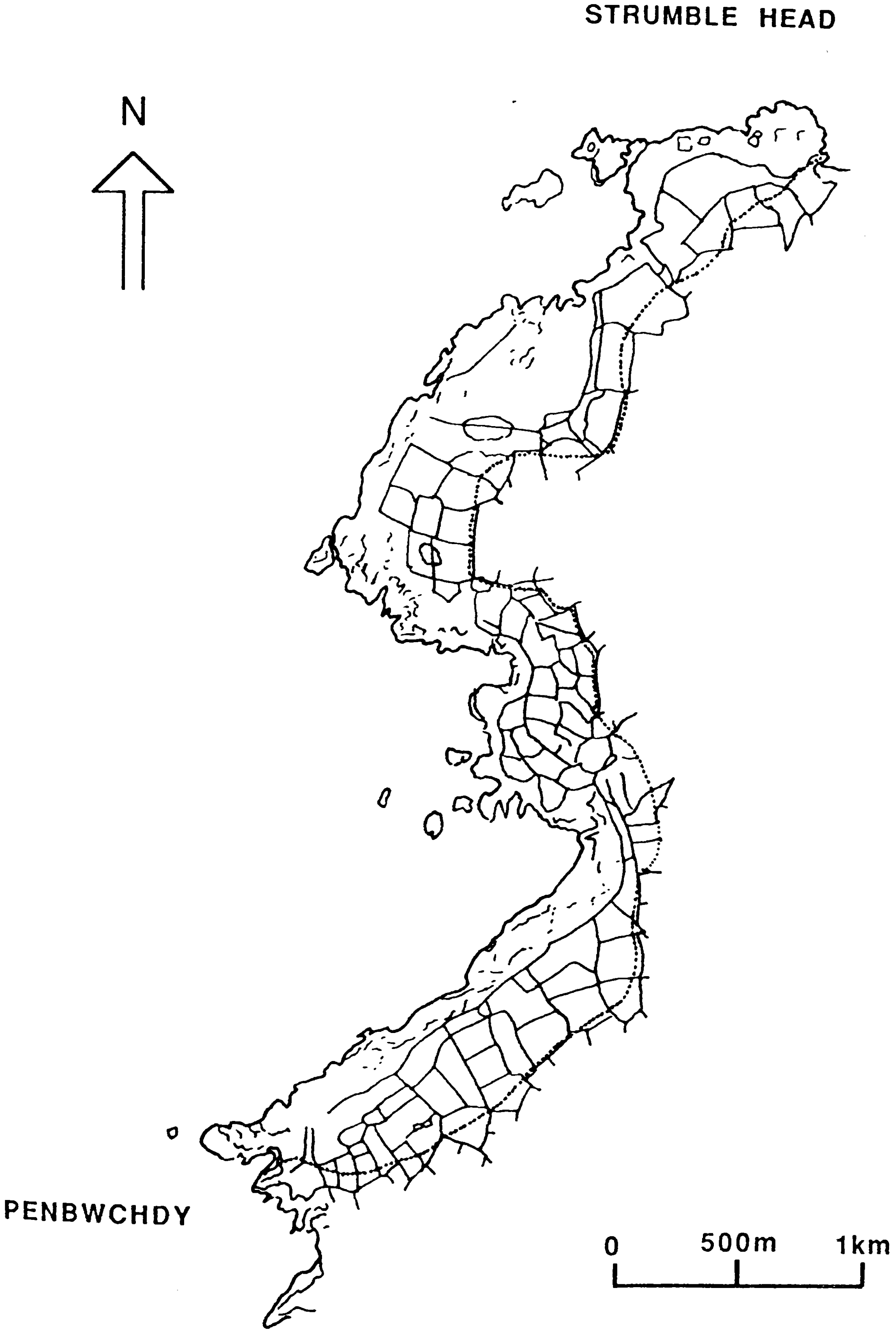
Figure 2.6c

Study area W1: Cemaes - Pen-yr-Afr section. Dotted line delimits study range sub-areas were subjected to visitor pressure. Reliable figures for Mwnt, deriving from a NT carpark, show that over 5 years (1985-1989), the mean usage was 10,910 cars per annum (s.d. 1,178), peaking during school holidays, when good beach, public amenities and proximity to Cardigan make it popular with local people (E. Gwynn pers. comm.). No such facilities and no beach at Cemaes result in reduced usage: the path being mainly used by serious walkers: usually <25 per day in the summer (pers. obs.); the path is little used in the winter. At Mwnt, the beach and open spaces are popular with dog-walkers throughout the year, especially in the evenings, when walkers are rare everywhere.

STUDY AREA W2: STRUMBLE (Figure 2.7, and see Appendix VIII). Strumble Head lies to the west of Cemaes (5°02-06'W, 52°00-03'N). It has been formed by dolerite intrusions of igneous rock into Ordovician sediments. [Igneous headlands and eroded sedimentary coves form a typical geological pattern of the region (George 1970)]. Both Strumble and Cemaes are NW trending headlands with, therefore, predominantly SW and NE aspects. Cliffs climb to about 80m, and are bounded to landward by species-rich maritime heath and mixed agriculture. A popular Youth Hostel at Pwllderi attracts considerable usage to the area which diffuses around the headland, although this declines considerably in the winter when the Youth Hostel is closed. The study area (*ca*.275ha) was believed locally to support many (±6 pairs) of Choughs (R. Spicer pers. comm.) but only one pair bred (successfully) in 1988-89. Strumble Head is a nationally important 'sea-watching' site, and most observer-effort concentrates on this activity; but since my work showed that the resident pair of Choughs foraged over most of the area, it is possible that over-estimation has occurred (see Section 1.3.2), further emphasising the need for a colour-ringing programme in West Wales (Chapter 7).

Figure 2.7

Study area W2: Strumble Head - Penbwchdy. Dotted line delimits study range


STRUMBLE HEAD
N
PENBWCHDY
0
500m
1km

STUDY AREA W3: NEWGALE-SOLVA (Figure 2.8, and see Appendix VIII). Situated at the north of St. Bride's Bay, east of St. David's Head (5°08-13'W, 51°-51'N), the area is in a higher grade agricultural neighbourhood than the more upland areas W1 and W2. The coastline has a southerly aspect, characterised by two reef-like promontories: Dinas Fawr and Dinas Fach, both of which supported successful nest sites. The larger promontory, Dinas Fawr, was grazed in summer, and because of its aspect, receiving exposure from both the south and west, supported the most feeding sites (Appendix VIII). Dinas Fach lacked southerly exposure and was ungrazed. The cliffpath is very steep in places, climbing to *ca.*100m. Despite the promontories, it forms a more linear stretch of coast than the remaining three sites; the study area (*ca.*125ha) is elongated by the intensive agricultural hinterland. The landscape has been shaped and the promontories formed by intrusions of basic rock into the Ordovician System; sheer cliffs alternate with 45° vegetated cliffslopes, often scrub-covered.

STUDY AREA W4: MARLOES (Figure 2.9, and see Appendix VIII). The Marloes peninsula forms the south-western tip of Wales, opposite Skomer Island (5°11-15'W, 51°42-44'N). It comprises mainly a plateau about 40m high on a W-E axis near Dale and St. Anne's Head, and includes Gateholm Island - once a Chough nestsite (D. Saunders pers. comm.): total study area *ca.*257ha. The interior agriculture is largely intensive sheep and arable, but at the southern end there is a disused World War II airfield, currently used for grazing. The westernmost tip, known as the 'Deerpark' is a NT owned property managed for its natural history interest. There are plans to reintroduce grazing to Gateholm Island (S.B.Evans pers comm.). The geology is Silurian with contemporaneous igneous intrusions. Cliffs and steep cliffslopes dominate. The shaded northern sector shown

Figure 2.8

Study area W3: Solva (Solfach) - Newgale. Dotted line delimits study range

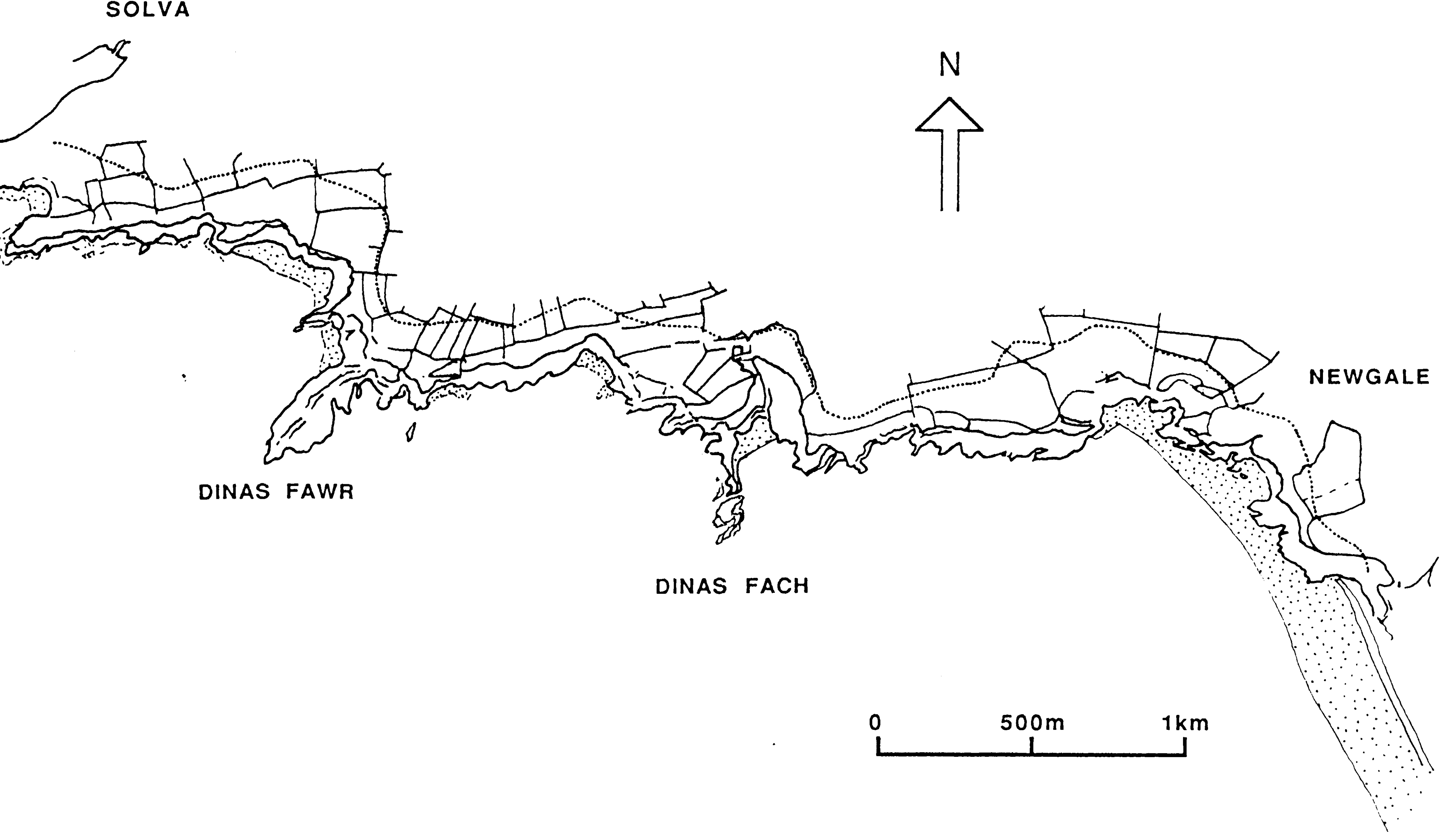
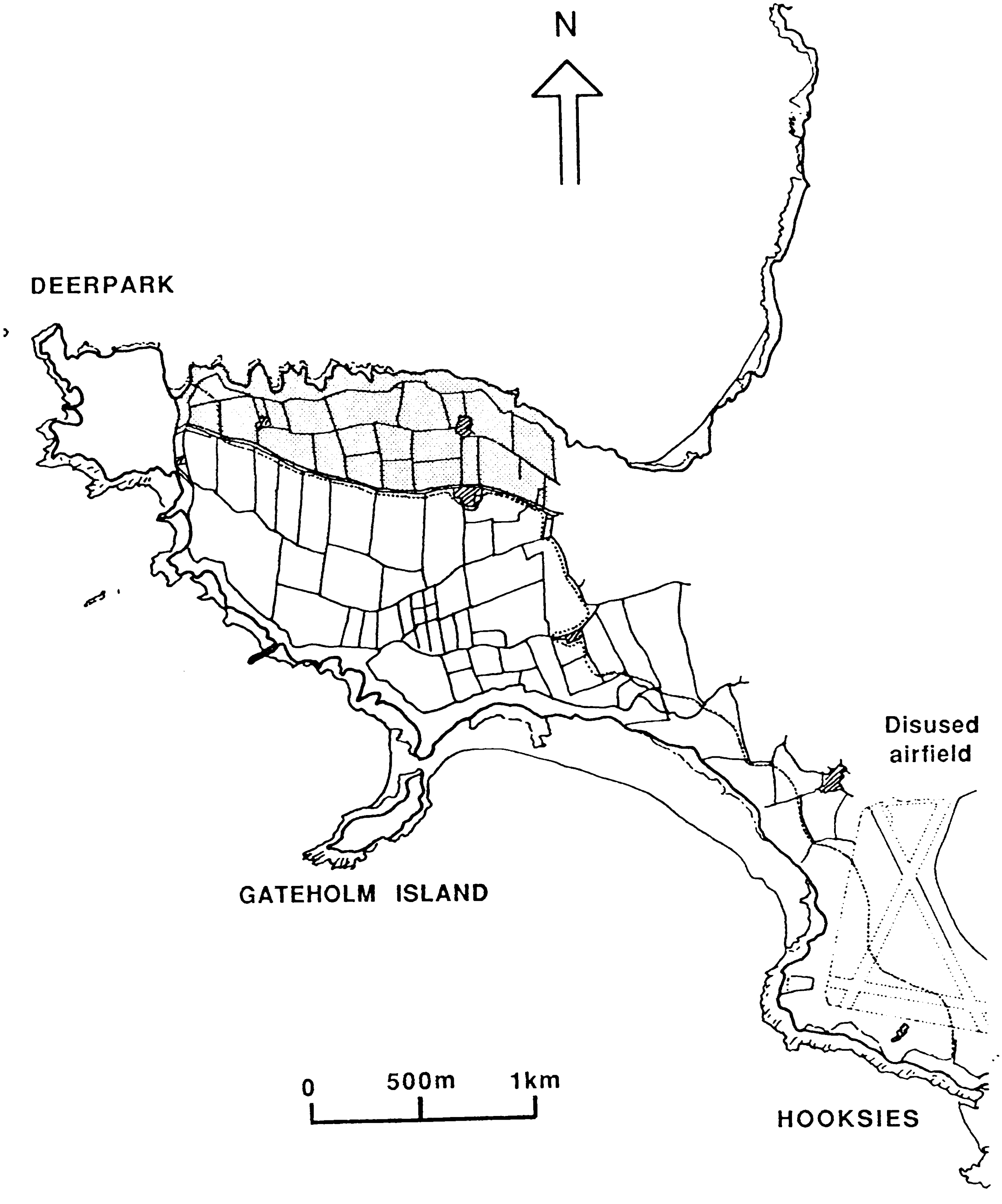

SOLVA
N
NEWGALE
DINAS FAWR
DINAS FACH
0
500m
1km

Figure 2.9

Study area W4: Marloes peninsula. Dotted line delimits study range. Shaded area indicates northern section, unused by Choughs during project time


N
DEERPARK
GATEHOLM ISLAND
Disused airfield
HOOKSIES
0
500m
1km

in Figure 2.9 (*ca*.70ha) was never seen to be used by Choughs during the entire study period.

2.3.3 THE CORNISH STUDY AREAS

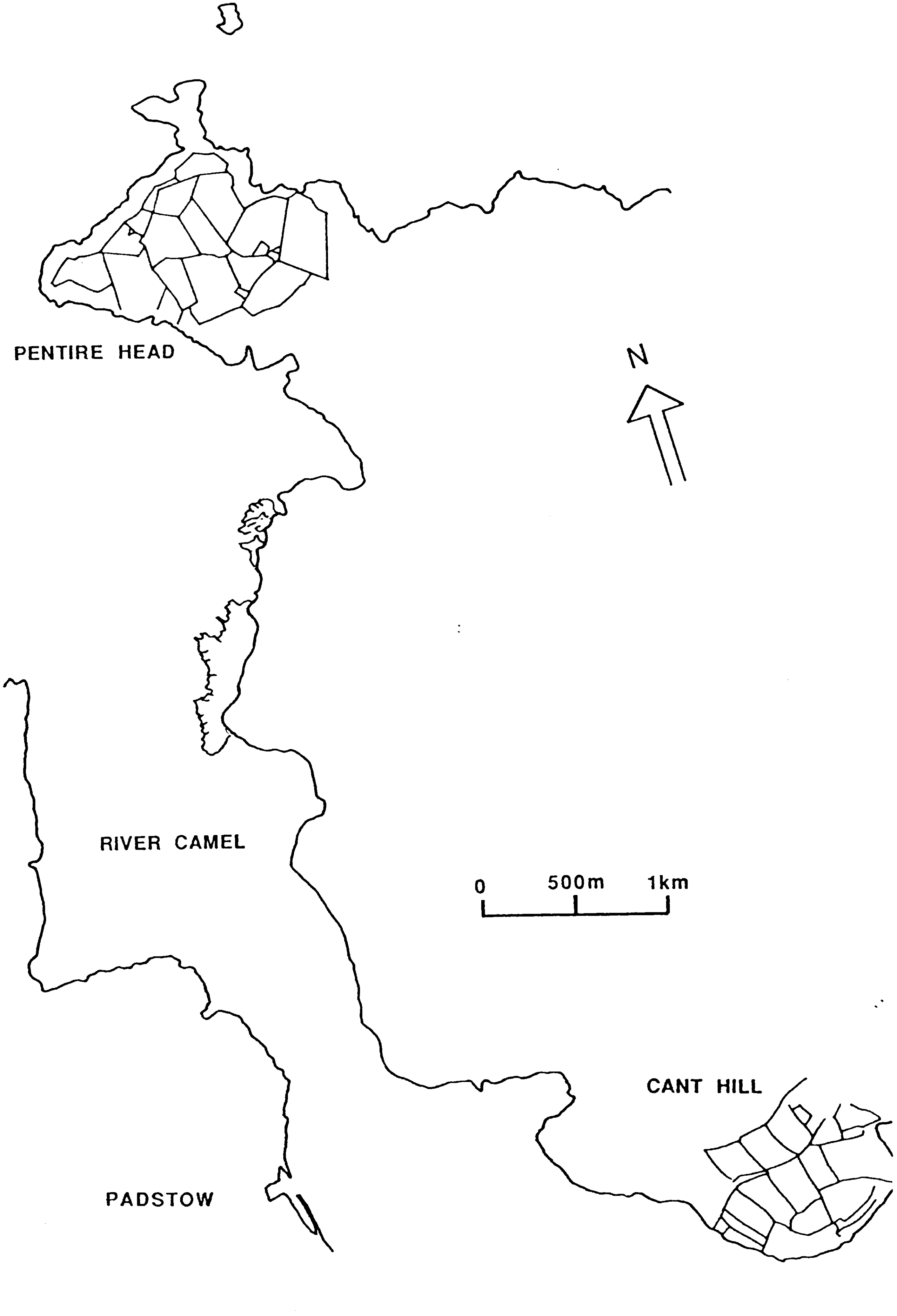
STUDY AREA C1: PENTIRE-CANT (Figure 2.10). Pentire Head (4°56'W, 50°34'N) was formed by volcanic extrusions of pillow lava >60m thick, and intrusions of greenstone into Middle Devonian slates (Edmonds *et al*. 1975). It has a NW orientation, akin to Study Areas W1 and W2, and is located on the Camel estuary north of Padstow. An unsubstantiated report records an unsuccessful breeding attempt at Pentireglaze ("a traditional site of great but unknown antiquity" (Penhallurick 1978) in 1947, and they certainly bred there between 1930 and 1944 (*ibid*). Ray in 1662 reported 'great flocks' nearby (Ray 1678). Pentire is a National Trust property. The interior is mainly mixed arable and sheep farming. The cliffs are *ca*. <60m high and rock outcrops and grass or scrub cover the moderately steep coastal slopes. It and nearby beaches are popular with visitors in the summer and with locals during weekends at all times.

The Cant section is a small site on the north side of the Camel estuary to the east of Pentire (4°54'W, 50°31'N), included to enable further invertebrate studies. Cant Hill is privately-owned, 75m high, with unimproved summit pasture and improved inland slopes, both grazed by sheep. *Ulex* scrub clothed the steeper slopes overlooking the estuary.

Figure 2.10

Study area C1: Pentire Head and Cant Hill.

Map showing eastern side of the Camel estuary. On the western side is Stepper Point and the town of Padstow


PENTIRE HEAD
N
RIVER CAMEL
0
500m
1km
CANT HILL
PADSTOW

STUDY AREA C2: WEST PENWITH (Figure 2.11). Most of the West Penwith coast was important historically for Choughs (see Figure 3.2). The particular site at Treveal, on the NW facing coast (5°33'W, 50°12'N), was selected because of recent occupancy by Choughs, disappearing *ca*.1870s (Penhallurick 1978), and for logistical reasons, NT ownership and residency of warden, and an agriculture and physiography superficially, at least, resembling Study Areas W1 and W2, including rough grazing by cattle.

STUDY AREA C3: THE LIZARD (Figure 2.12). The west side of Lizard Point (the most southerly part of Britain) is historically important for Choughs. The Predannack cliffs (5°15'W, 50°°0'N), south of Mullion, is an area where Choughs were in 'tolerable abundance' (1856; see Figure 3.2) but possibly gone by 1870 due in part to the activities of egg collectors (Penhallurick 1978). Predannack is owned and managed by conservation interests: NT and NCC. The geology of the Lizard is amongst the oldest, most complex and interesting in Britain (Edmonds *et al*. 1975). The Predannack cliffs are basically hornblende-schists of *ca*.50m and levelling into a plateau of largely unimproved or semi-improved grass with heath and scrub elements. The more intensively managed fields were down to either improved cattle-grazed grass or arable. Grazing within the study area was by equines and sheep.

Figure 2.11

Study area C3: Treveal cliffs, West Penwith. Map showing northern section of the West Penwith coast near sampling area plus associated field system

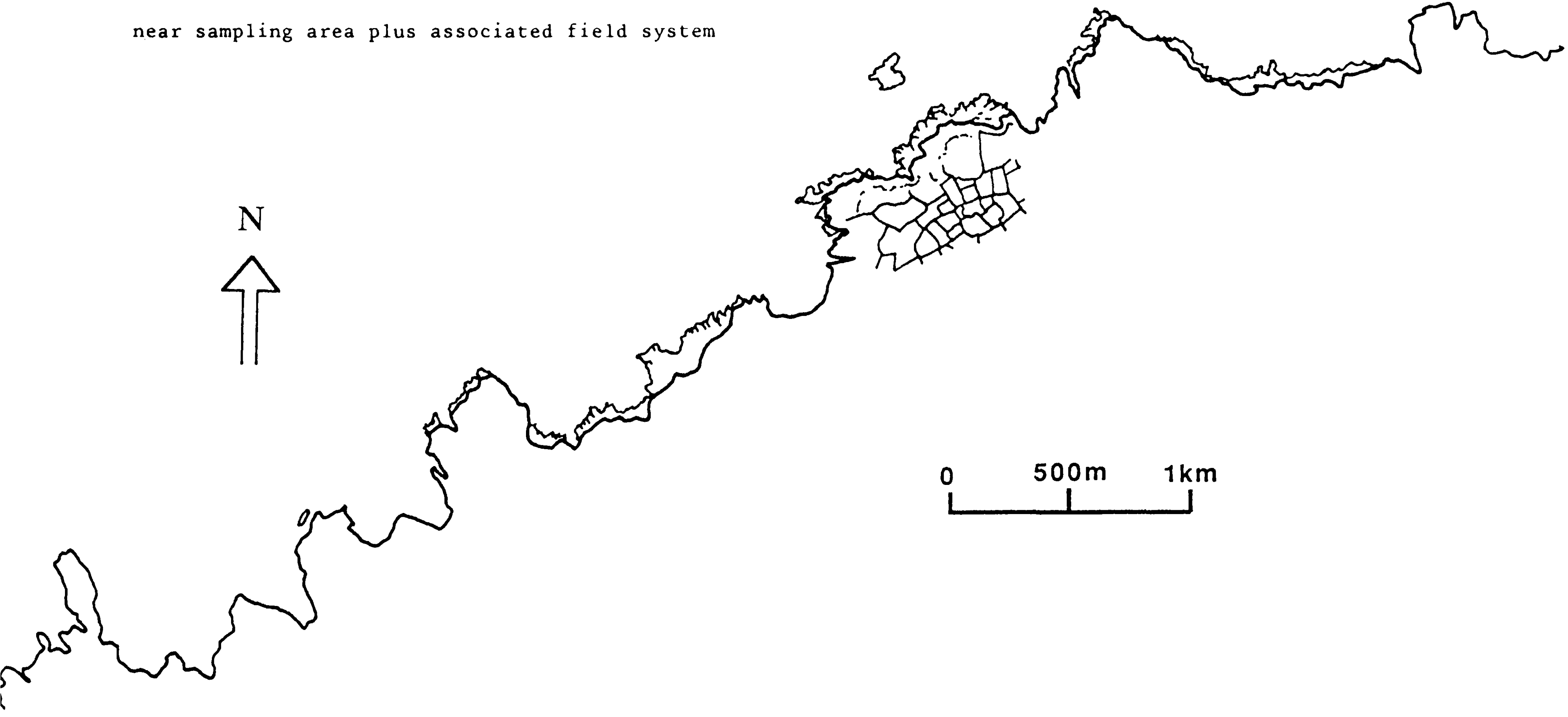
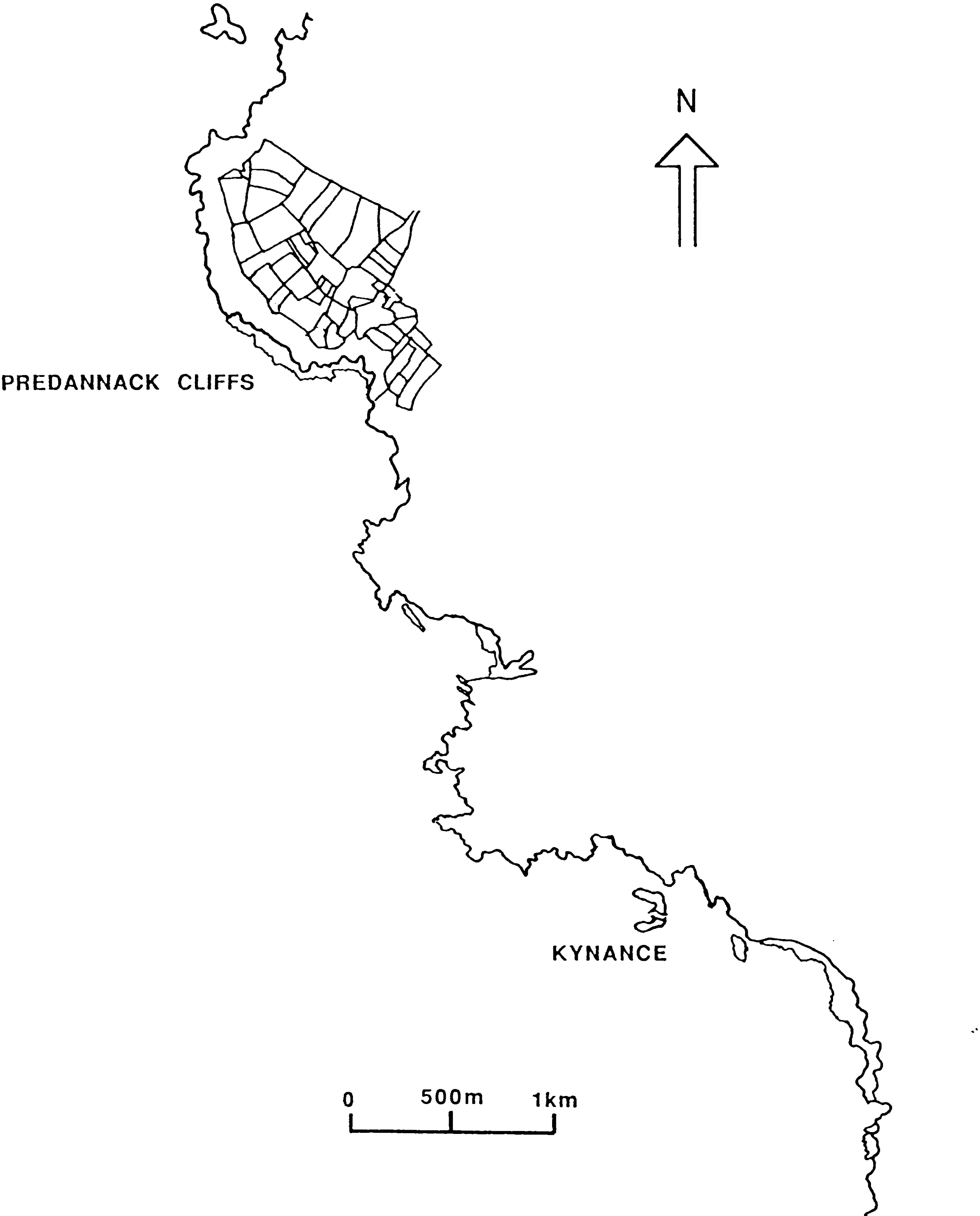


Figure 2.12

Study area C4: Predannack cliffs. Map showing western section of the Lizard coast near sampling area plus associated field system


N
PREDANNACK CLIFFS
KYNANCE
LIZARD POINT
0
500m
1km

2.4 HISTORICAL HABITAT ASSESSMENT

The Chough's decline and disappearance from southern England is investigated mainly by reference to the historical literature (Chapter 3) and an assessment of changing land-use practices as revealed by tithe surveys (4.5 & 4.6). Owen (1985) examined the historical literature for evidence of the decline in England, paying particular attention to Cornwall and Wales. I have added a little new evidence and reinterpreted some of his data.

The Tithe Apportionments of the 1840s provide, with caution, a reliable insight into contemporary land-use (Kain & Holt 1981) for both Cornwall and Wales. The coastal 1km^2 mapped in the original habitat assessment (see Section 2.2, Figures 2.2 - 2.5) were reanalysed from tithe data to provide a measure of the quality and rate of habitat change. The maps were rasterized similarly so as to enable direct comparison although the available information was of a far less precise nature: broad variables such as 'pasture', 'arable', 'furze' etc. forming the parameters (see Figures 2.13 & 4.3). In addition to the map data, there were also aggregated acreages available for each parish, and these were compared to recent MAFF (Ministry of Agriculture, Fisheries & Food) census returns.

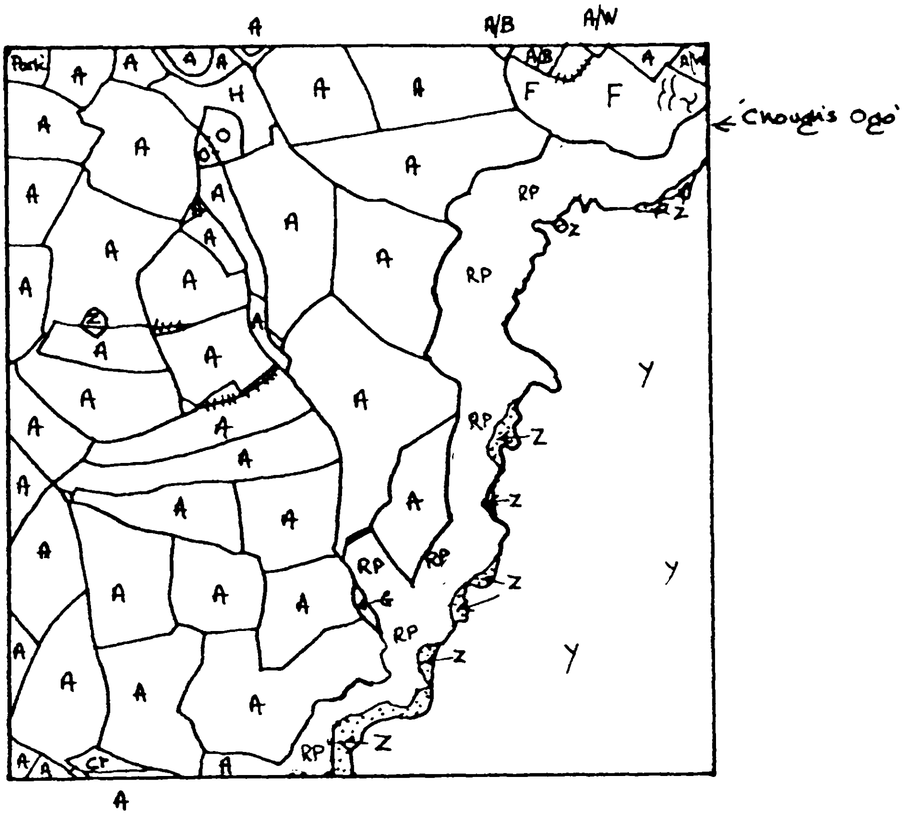

A
A/B
A/W
Park
A
A
A
A
A/B
A
A/W
H
A
A
F
F
'Chough's Ogo'
A
A
O
O
A
A
RP
Z
Z
A
A
A
A
RP
A
Z
A
Y
A
A
A
RP
Z
A
Z
A
A
A
A
RP
RP
Z
Y
A
A
A
G
RP
Z
A
A
A
Y
RP
Z
A/A
Cr
A
A

Figure 2.13

Example of 1km sq. annotated from tithe map data *ca*.1840. The cave 'Chough's Ogo' probably identifies an historic nesting site (see 2.3.1). Scored out hedge lines denote hedge or bank removal

Key:

A	Arable
B	'Banks'
Cr	Croft
F	Furze
G	Garden
H	Homestead
O	Orchard
RP	Rough pasture
W	Waste
Y	Sea
Z	Undefined

2.5 BIRD OBSERVATIONS

2.5.1 THE DETECTABILITY OF CHOUGHS

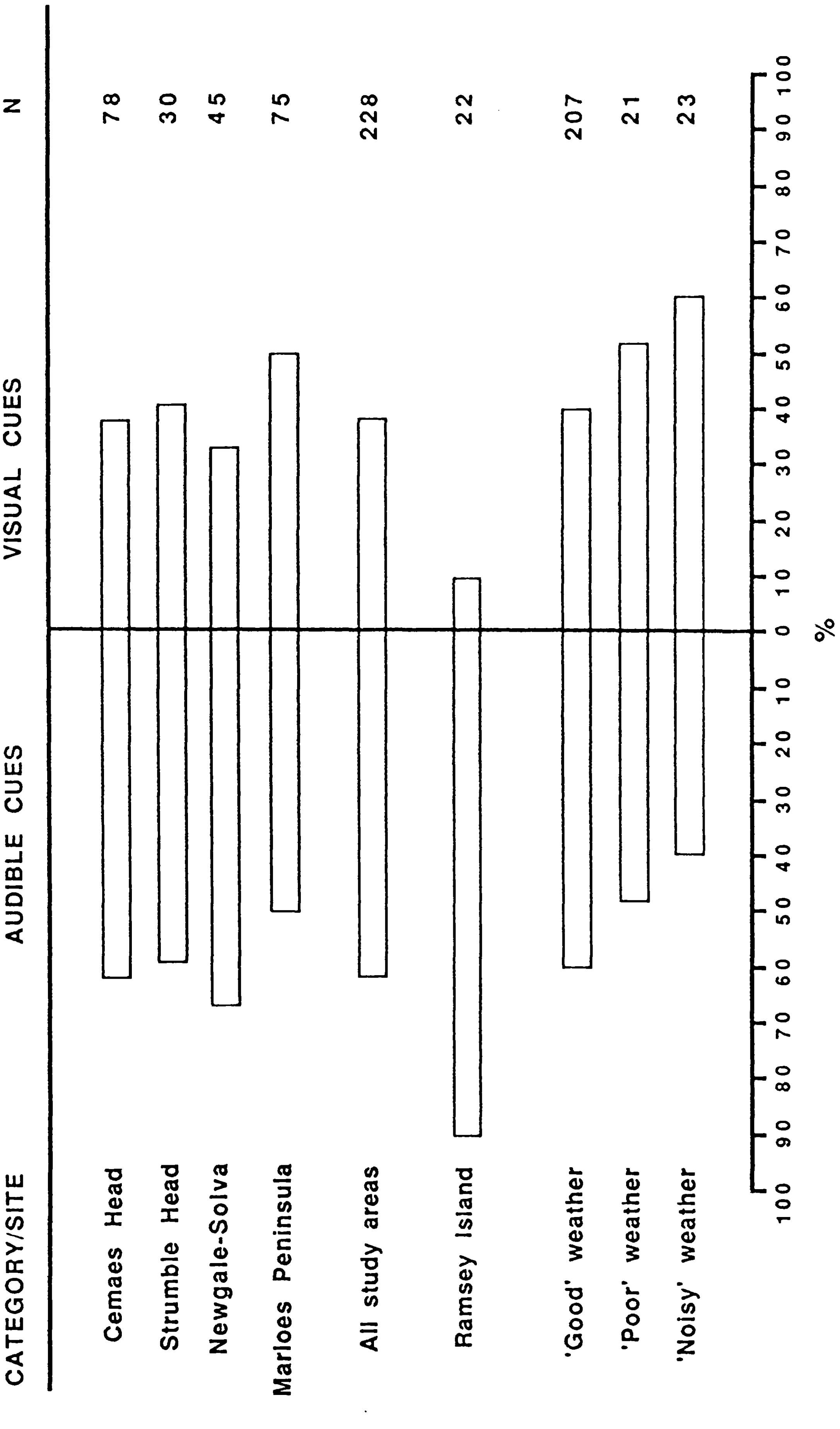
Physical location of the subject within the time available was problematical. Bullock (1980) and Roberts (1985), working respectively on South Stack and Bardsey island reserves to the north (Figure 1.2), were able to employ transect routes and 'pursuit days' "when groups of Choughs were watched all day." Roberts mentioned the advantages of "so many observer-hours on such a small and discrete area." In contrast, I occasionally spent entire days without locating a single Chough, and initially the concept of pursuit was replaced by one of dedicated search time (DST) (2.5.2).

The bird-watching literature claims that the Chough's distinctive cry (1.3.1) often draws attention to it. It would clearly be useful to know if this encouraged a bias: with negative records being interpreted as actual absence of birds rather than mere non-visibility, and whether poor visibility, due to weather conditions, decreased search success. Consequently, all presence cues - visible (VC) and audible (AC) - were recorded for one year from June 1988 in order to check their relative frequencies. To prevent a 'learning' or 'knowledge curve' affecting the results, only 'surprise' cues were counted, and those resulting from nest-watching or from where birds were expected were omitted.

The data presented in Figure 2.14 support the fieldguides. In all conditions, 63% of surprise encounters (n=228) were AC initiated. In poor visibility/bad weather, when the proportion might be expected to increase, the reverse applied and ACs decreased to <50% (n=21). This can possibly be explained by Choughs sheltering and remaining quiet in ad-

Figure 2.14

Proportion of Chough observations initiated from audible cues (AC) and visible cues (VC) by study area and different weather conditions


CATEGORY/SITE
AUDIBLE CUES
VISUAL CUES
N
Cemaes Head 78
Strumble Head 30
Newgale-Solva 45
Marloes Peninsula 75
All study areas 228
Ramsey Island 22
'Good' weather 207
'Poor' weather 21
'Noisy' weather 23
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
60
70
80
90
100
%

verse weather (Borlase 1758; and see Section 6.3.1). During 3 days of observation on Ramsey Island in July 1989 (Appendix V) in excellent conditions, and in a situation comparable to the island reserves of Bullock and Roberts, 20 of 22 (91%) 'surprise' encounters, were of AC origin, possibly reflecting the higher density and/or better weather.

To establish whether the converse applied, *i.e.* did very windy or 'noisy' conditions reduce the number of ACs, cues in a wind velocity estimated as >6 on the Beaufort Scale (n=23) were subjected to a chi-square test; 14 (61%) were of VC origin ($X^2 = 1.608$; d.f. 1; N.S.). Although a small sample, the value is equivalent to that for ACs in 'good' weather, suggesting that there is, at most, only a low element of bias relative to weather conditions and, from the Ramsey data, densities of birds. Interestingly, at wind force 6, the AC:VC ratio was almost exactly equal.

It is possible that AC induced 'sightings' would have been subsequently detected by observer effort, but it cannot be known how many sightings were missed altogether; the data include only subsequently confirmed sightings. In conclusion, detection was ~~usually successful~~ probably independent of weather and topographical conditions, but search time was affected.

2.5.2 GENERAL OBSERVATIONS

Due to the low density of birds, scattered sites and initial poor success, the pursuit concept was replaced, as stated, by DST, in which an attempt was made to strengthen the evaluation of time budgets by assessing non-usage of ground patch types. By relating non-usage to usage and examining the results in relation to the availability of those patch types, negative data might increase in its significance and be less wasteful of effort. However, if these results were to be meaningful, it was necessary to know how Choughs spent their time when not under observation, and whether they were unobserved due to observer inefficiency, topography, habits or climatic factors, *e.g.* sheltering in hot/cold/wet/windy weather (see Sections 2.5.1 and 6.3.1).

Rigorous interpretation of negative records was confounded by these variables, but, with a few notable exceptions, it was found that due to increasing knowledge of the birds' habits, negative records *per se* became virtually non-existent, and it was possible ultimately to drop DST and revert to Ian Bullock's (1980) pursuit concept. However, since time spent in the field on different inquiries was always logged, negative periods were available, if needed, by the simple equation: $N_{-ve} = N - N_{+ve}$.

As stated, study sites were visited every 6-8 weeks. The whereabouts of Choughs was ascertained by routine searching of the ranges around known nest sites, which were regarded as focal centres. Family roosting occurs at or near nest sites in June and July (Williamson 1959; Cowdy 1962, 1973; Roberts 1985), and it is possible that low-density populations retain this behaviour for longer (pers. obs., *cf.* Still 1989). Methodical searching radiating away from foci was carried out until successful or it was assumed that the birds had been missed; the procedure was repeated until it was assumed that the birds were not present, whereupon wider areas were searched. At the outset, some entire days were negative. Subsequent information helped to explain these events which occurred only during the winter, due to shorter days, poor weather and reduced or temporarily non-linkage with the nest/roost place.

When found, pursuit commenced. Birds were observed by a 9x35 binocular or a x20-60 zoom-lens telescope. Every effort was made not to disturb the birds (and see p.165). Occasionally, it was unavoidable, as for example when the observer happened to be in a location desired by the Choughs. However, the subjects were generally found to be sufficiently 'trusting' to allow approach to *ca*.60m (see also Section 6.3.3). Generally the birds were less approachable during the winter and autumn, presumably because they were not constrained by reproductive duties.

2.5.3 ACTIVITY PATTERNS

Activities and habitat selection were recorded, either in a notebook or on to a portable tape-recorder. The location and nature of all foraging events were noted by habitat variables (Table 2.2; see Chapter 4). Major categories tended to be one (or more) of the following: (i) 'broad' categories, such as 'maritime cliff' which, unqualified, denoted an absence of more precise information (occurring most often when birds foraged out of direct view); (ii) homogeneous habitats, *e.g.* 'improved pasture', 'dung' etc.; and/or (iii) prime feeding habitats, such as 'exposed substrate', 'therophyte zone' etc. Subdivisions refined the major categories so as to enable a precise description of resource use. In practice, categories and subdivisions were often combined. Supplementary

Table 2.2 Habitat variables; bold type indicates cliff/non-intensive agriculture (see Section 4.3.1)

	Major categories	Subdivisions	Comments
1	**MARITIME CLIFF**		unspecified
a		Top (eroded zone)	>horizontal <vertical
b		Edge (eroded zone)	<horizontal >vertical
c		Slope	usually grass clothed
d		Scree	unstable
e		Crevice/rock	>50% rock
2	**SPARSE VEGETATION**	open ground	therophytes (winter annuals) etc.
3	**ROCK/VEGETATION**	interface	<50% rock
4	**SHALLOW EARTH**		
5	**EXPOSED SUBSTRATE**		
6	**MARITIME GRASS**		[1] see footnote
7	**MARITIME HEATH**		
8	**SEABIRD FLORA**	Cliff community	e.g. *Lavatera arborea* *Beta* sp.
9	**ROCK OUTCROPS**		
10	**PATH**	Actual or influence	trampled/eroded ground
11	**ANT-CREATED**	Mounds	habitat shaped by ants
12	**WALL/HEDGEBANK**	'Mini-cliffs'	grazed/short/open vegetation
13	**PERMANENT/ OLD GRASSLAND**	unimproved	natural/semi-natural[1]
14	**OLD-IMPROVED GRASS**	Semi-improved	ca. > 7yrs old[1]
15	IMPROVED GRASS		ca. < 7yrs old inc. drilled/reseeded leys[1]
16	STONEY SUBSTRATE		
17	SPECIES-RICH	Herb-rich	indicative of 13 or 14 etc
18?	STOCK TYPE		unknown
a		Cattle	}
b		Sheep	}
c		Equines	} or combination
d		Rabbits	}
19	**DUNG & DUNG-FEEDING**	qualified by current, recent & mature/old	}{ not mutually exclusive - }{ also indicates age of }{ grazing
20	**ROUGH-GRAZING**		
21	ARABLE		Cereal grain
22?	OTHER AGRICULTURE		unspecified, not a-e
a		Ploughed	
b		Silage/hay aftermath	
c		Roots/brassicas	
d		**Ruderal/neglected**	atypical
23	**PROXIMITY OF NEST**		{ qualifies habitat
24	**PROXIMITY OF ROOST**		{ selection

---

[1] Vegetation heights were recorded by the parameters: short <25mm; medium 25-50mm; long-rank >50mm; variable.

data were collected, notably on prevailing weather conditions. Additional data were supplied by local naturalists who recorded observations on feeding incidents to the same criteria. This helped to extend the field period within the area covered.

Habitat usage and selection was enhanced by behavioral observations obtained by instantaneous sampling of focal animals as recommended by Altmann (1973). On every hour and half-hour, plus a first opportunity in case of sudden departure, detailed behavioral observations were taken by telescope over periods of one minute duration. To overcome the bias inherent in *ad lib* sampling, when two or more birds were in view, the nearest was selected or, if equidistant, the left-most. These 'focal minute' data were dictated onto audio tape and later transcribed to the nearest second by digital stopwatch. Behavioral data were gained from different habitats on vigilance (frequency and number of scans; see Appendix IX); feeding, including an estimation of success rates and prey; movements on the ground; flights; and other behaviours including resting, maintenance, interactions etc (Chapter 6).

'Feeding' included both *foraging* - actual feeding, with head down or horizontal and eyes scanning the ground (Feare *et al.* 1974), and *hunting* - inclusive of all other activities integral to foraging, *e.g.* vigilance movements and locomotion between foraging patches. The other principal behaviours were associated with breeding (courtship, nest-building, incubation, care of young), inter-specific interactions, maintenance activities, resting, roosting and sheltering etc.

Usually pursuit was undertaken for at least two half-day periods at each study area per visit. Usually they would include morning and afternoon periods on separate days: the former beginning at dawn, and the latter ending when the birds went to roost. Profitable morning periods were occasionally continued into the afternoon if circumstances permitted, in order to compensate for negative searching.

Prevalent weather conditions and their changes were recorded throughout observation periods. Cloud cover was measured in increments of eighths: 0/8 (=no cloud) to 8/8 (=overcast). Temperature was measured in 5°C bands: 0 = <0°C, 1 = 0-5°C, 2 = 6-10°C ... 6 = >25°C. Wind was measured on the Beaufort Scale: 0 = Calm ... 9 = Strong gale; and wind direction was also recorded using conventional compass points. Precipitation was registered on the following scale: 0 = dry, 1 = mist/light rain, 2 = steady rain, 3 = Heavy rain, and 4 = hail/snow.

During pursuit, feeding sites were marked for later sampling, and faeces were collected whenever possible. Evidence of digestion in Choughs can be seen after about two hours (Bullock 1980, and see Appendix X). To help matching of remains to feeding sites, only fresh faecal samples were taken. Occasionally, older samples were collected to check the prey assemblage. After bird observation was complete, a further day (or part thereof) was set aside for invertebrate sampling. Therefore, a minimum of 3 days was usually spent at each study area per visit. Unfortunately, no accessible roost site was found, and no pellets were examined from Welsh birds (but see Appendix IV).

2.5.4 INVERTEBRATE SAMPLING

Pursuit data, in particular feeding observations, were supported by invertebrate sampling. Feeding sites were visited immediately on departure of the birds and sampled directly or marked for later sampling. There were often clear signs of Chough activity: probe holes, faeces or disturbed ground and vegetation. The primary objective was to identify the selected prey. Sometimes this was obvious: *e.g.* anthills, dung fauna, diptera colonies, tipulid larvae, earthworms and cereal grain, and some of these foods could clearly be seen to be taken during bird observation. At other times, prey was not obvious, such as when Choughs were feeding opportunistically. Feeding areas were sampled as near the feeding point as possible and compared to 'control' sampling on adjacent ground which appeared similar yet unused, either within the same complex or adjacent to it (see Section 5.2.1).

Soil cores measuring 8x6cm were extracted unless prevented by geology, in which case an equivalent volume of substrate was taken by knife or trowel. Except when a prey focus was obvious, a minimum of 3 samples was taken from feeding sites, where feeding was scattered within a patch, a transect of 5 core samples at 1m intervals was taken (Figure 2.15); 5x1m transects were also used when sampling in unused habitats. In agricultural fields or where an edge effect might have confounded the results, the transect was begun at a point 25m from a field corner and 25m at right angles into the habitat being sampled (Figure 2.16). To eliminate observer bias, the precise starting point was randomly selected and the transect line directed towards the nearest coast point (after Hughes 1962).

Figure 2.15

Transect of 5 x 1m soil cores (8 x 6cm) taken for invertebrate samples

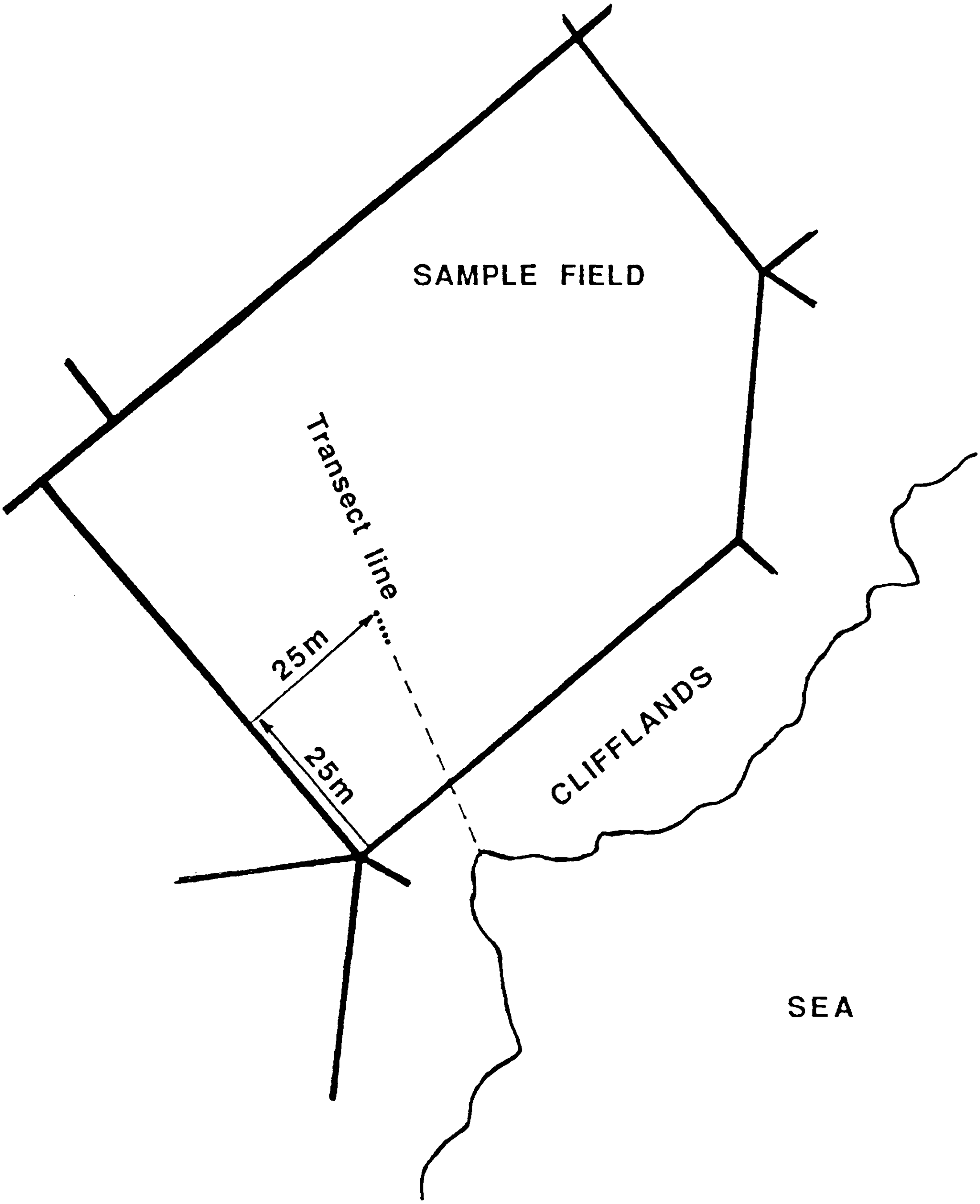

SAMPLE FIELD
Transect line
25m
25m
CLIFFLANDS
SEA

Figure 2.16

Strategy for arbitrary sampling of substrate in field (or monotypic patch), to avoid edge effect. Dashed line denotes most direct route to coast

2.5.5 FAECAL SAMPLING

Whilst the examination of cast pellets from both raptors and corvids has been quite widely practised (*cf.* Dugmore 1986, Howes 1975, and Yalden & Warburton 1979), even to the extent of identifying fossil remains (Girling 1977), much less research has been carried out with faecal material (*cf.* Ralph *et al.* 1985). Moreby (1987) has applied the technique to examine the diets of gamebirds, and Green & Tyler (1989) have studied faecal evidence from captive Stone curlews. To some extent, progress has been limited by the problems inherent in the identification of fragmentary material, although, for many years, paleontologists concerned with insect remains from Quaternary deposits have been dealing with such material with considerable success (for review, see Buckland & Coope 1990). Kenward (1976) pointed out the contribution which bird faeces made to archaeological insect assemblages by a study of modern building gutter assemblages in York.

In this study, faecal evidence provided direct and irrefutable evidence of Chough diet, and considerable effort was expended in both collecting samples and identifying the surviving components (5.2.2).

3 STATUS AND DECLINE

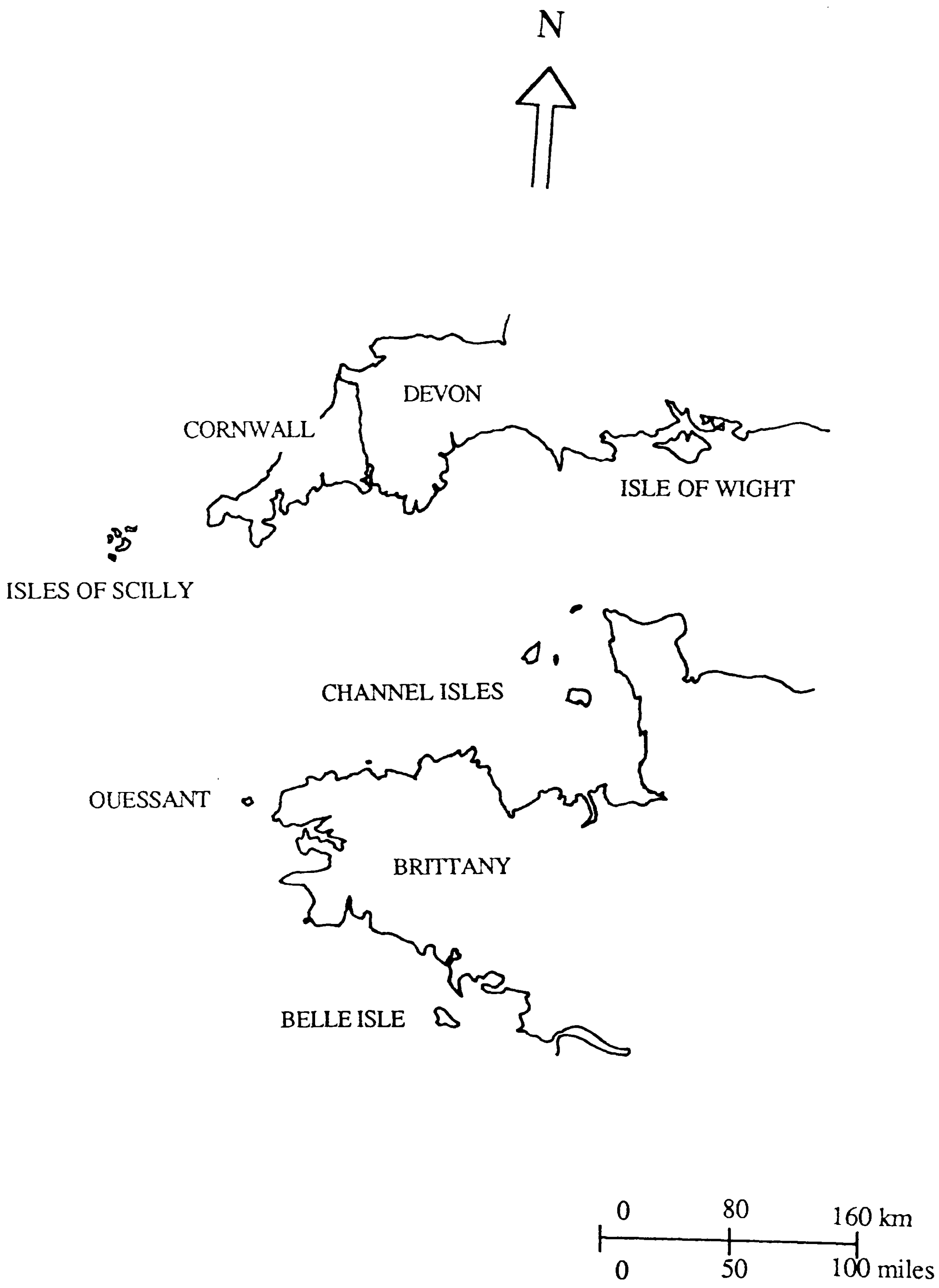
3.1 INTRODUCTION

In order to understand the comparative scarcity of the Chough in Britain, and help its conservation, we need to know why previous declines occurred (Darke 1971, Coombs 1978, Monaghan 1989). Data which might shed light on the Chough's past status and decline are scattered throughout a wide range and variety of historic sources. Although they may not be quantitatively assessed in critical detail, it would be foolish to overlook potentially valuable information where it does occur and where the source is reliable. This chapter, therefore, reviews the historical evidence which relates both directly to the demise of the Chough, principally in southern Britain but also to the French zoogeographic region to the south (Figure 3.1), and to those environmental factors which might have influenced it.

The historical literature, examined previously by Bullock *et al.* (1983b) and Owen (1985), shows that the Chough was once widespread on the southern coast of Britain, and also bred at east coast locations. Fossil evidence, from 130,000BC, testifies to occurrence in Yorkshire and inland in Derbyshire (Owen 1985), and in Europe it was widespread when steppe conditions prevailed (Guillou 1981); Guillou suggests that when steppe was succeeded by forest, the Chough became dependent on montane and coastal regions, and, subsequently, on primitive farming practices. Historical evidence from the Isle of Man dates back to AD90 (Cullen & Jennings 1986). Supportive evidence from inland or eastern sites in England is sparse but breeding currently occurs in Snowdonia and at a few locations in mid-Wales (Bullock *et al.* 1985). Artefact sites are unknown

Figure 3.1

Locations of south-west England, North France (Brittany) and the Channel Islands


N
DEVON
CORNWALL
ISLE OF WIGHT
ISLES OF SCILLY
CHANNEL ISLES
OUESSANT
BRITTANY
BELLE ISLE
0
80
160 km
0
50
100 miles

from historic England, and very rare in Wales; one pair used to nest in a castle at Llangollen in the early 1800s (Forrest 1907), and "in former days" (Mathew 1894) the Chough was said to nest in a ruin at St Davids (Pembrokeshire) 1km from the coast. In Scotland, until the early C19, it "was comparatively abundantly distributed in many inland districts" (Buchanan 1882, and see Warnes 1983). The west of Ireland is the stronghold for the Chough but unfortunately lies beyond the scope of this study. It has declined sharply in Northern Ireland (Bullock *et al.* 1983). There is a real need for a full ecological study of Irish Choughs, and this has begun with the formation of the Northern Ireland Chough Habitat Enquiry (BTO 1990). The first all-Ireland census (Ussher & Warren 1900) was updated by Cabot (1965) and Bullock *et al.* (1983b).

In Great Britain, a general decline is suggested by all accounts post-C18. Dixon (1888) wrote:

> "From causes that baffle all conjecture to explain them, this handsome rock-bird is gradually becoming rarer and rarer in this country. Formerly it had its noisy colonies on many an inland cliff, but at the present day it only frequents a few favoured localities on the rock-bound coasts. It may be that the Jackdaw is slowly driving out the Chough, or the spread of C19 civilisation is too much opposed to its retiring habits and love of solitude. Whatever be the cause of its disappearance, we have now to repair to the wildest and most inaccessible parts of the rock-bound coasts if we wish to see the handsome Chough at home."

Malan (1891) remarked: "Considering their former plentitude, their present scarcity is not an altogether easy matter to account for." Causes given were: "(1) Jackdaws swarming round the cliffs, harming and usurping their nesting places; (2) trapping and shooting in former days; and (3) robbing nests and taking young and eggs" (quoted in Palmer, 1950s undated pamphlet, *The Old Cornwall Society*) (3.4).

Without quantitative data it is impossible to assess pre-decline status and distribution accurately. That the Chough was a familiar species is suggested by the frequency with which it appears in Welsh and English heraldry, on insignia and family crests etc., but its striking looks could have made it popular as an heraldic device on the edge of its range. Rarity itself attracts attention and would increase the esteem in which it was held. Upton (*ante*1446, trans. from the Latin *ca*.1500, publ. 1651) comments:

> "some of their (Cornwall's) most ancient families bore these birds in their coat-armour. Now to shew that these gentlemen made no contemptable choice of their 'bearing', it must be remembered that the Cornish Chough is the most graceful, slender and genteel of the crow kind" (quoted in Darke 1971).

Carew (1602) stated "I mean, not the common daw, but one peculiar to Cornwall." That the Jackdaw and Chough merited such splitting further suggests that the latter was not some little known oddity though it was clearly far less common. Upton states:

> "Ther be dyverse kyndes of thes byrdes for some be blacke in ther bylles and legges, wherof ther is great abundance; and some be rede in ther bylles and fete, which be smaller than the other and but few in number. They be most in cornwall..."

Rarity did ensure a fairly reliable recording of actual disappearance. In mainland Scotland, the historic status of the Chough will repay fresh examination. Baxter & Rintoul (1953) assembled much of the data and remarked on the "parallel decrease" in England. It would be interesting to see how Scottish data correlate with bioclimatic, socioeconomic, geographic and other independent variables, and this is currently underway (McKay in prep.).

The Chough operates within a narrow ecological niche (Bullock *et al.* 1985). It is likely that human activity "where it (the Chough) is at the mercy of changes in land use" (Curtis *et al.* 1989), has had a substantial effect (see Chapter 4).

3.2 BACKGROUND TO STUDIES IN SOUTHERN BRITAIN

In ancient natural histories and travel journals the Chough received more attention in Cornwall than anywhere else. This was due, in part, to the belief promulgated by Carew (1602), mentioned above, that the species was "peculiar to *Cornwall* ... there-through termed a *Cornish chough*"; "deservedly so-named among the moderns" according to Borlase (1758).

Owen (1985) concisely explains the etymology of the name 'chough':

> "Until 1402, forms of the word Chough were the only words used in English to describe the Jackdaw. The emergence of the word daw in the 15th century meant that until the 17th century, both Chough and daw were used to describe the Jackdaws. ...from c1449 Choughs were described by the form Cornish Chough."

Penhallurick (1978) provides a good review of the early records. He claims that Cornwall was the type locality of the Chough since Linnaeus obtained his specimens from England and also received mineral specimens from Cornwall "where was there more natural for him to obtain a specimen?". If so, there is some justification for Cornwall's claim to the nominate race, which found expression throughout Britain. Linnaeus related the Chough to the Hoopoe (see Section 1.3.1). Tunstall, in his *Ornithologia Britannica* of 1771, elevated *Pyrrhocorax* to generic status, and subscribed to the vernacular 'Cornish Chough'. In Wales, it was (and still is) occasionally known as '*bran Cernyw*'; in Scotland, '*Cornwall kae*' (Sibbald 1684) or 'Cornish Chough' persisted until at least as recently as the 'New Statistical Account' of 1839 (Baxter & Rintoul 1953). The practice has been adopted even by the authors of *The Birds of the Soviet Union* (Dementiev & Gladkov 1954)!

Taxonomic confusion existed regarding *Pyrrhocorax pyrrhocorax* and its Alpine congener. Turner (1544), who is not known to have visited Cornwall, and spent many years on the Continent, possibly began the confusion when he wrote his "succinct account of the principal birds mentioned by Pliny and Aristotle". Turner would certainly have been more familiar with Pliny's bird 'of *luteo rostra* (yellow beak)'. Belon (1555) described the species correctly but his accurate account was overshadowed by a major work, published in the same year by Gesner, which was to become the standard work of reference throughout Europe. Gesner (1555) obtained his information about choughs from Turner and Belon. Possibly influenced by his personal knowledge of *graculus* alone, he accepted Turner's account and additionally repeated the myth that the bill changes colour from red in summer to yellow in winter. In Section 1.3.1, I mentioned the possibility of confusion, between immature Red-billed choughs and adult Alpines due to the colour of bill and legs; although this would be more likely to cause a confusion the other way. "Such was the influence of Turner and Gesner that it was possible for an undiscriminating writer to become hopelessly confused long after Bellon and Carew had described the Cornish chough correctly" (Penhallurick 1978). For example, in the *Itinerarium Mundi* (Mundy 1654) is found the following description:

> "The Cornish Daw, breeding in shafts of Tynne [tin mines] seldom seine elsewhere; it hath long yellow legs and a yellow bill; the body black, it hath a note like a chough [Jackdaw] but pleasanter".

Penhallurick wryly points out that Mundy was "a Cornishman to boot". He is doubtful that Choughs nested in mine shafts in Cornwall, and yet Darke (1971) gives documentary evidence that this did occur. Stewart (1928) reports that pairs "in two widely separated and remote parts of Lanarkshire [were seen] emerging from old pit shafts", they certainly use such sites in Wales (*e.g.* Breeze-Jones 1959, Roberts 1978, and pers. obs.), and a variety of natural shafts (*e.g.* 'blowholes').

Mundy's passage highlights the 3-way confusion which now besets historical review concerning the two *Pyrrhocorax* species and the Jackdaw. Camden (1610) was more discriminating: while not knowing the British distribution of the Chough, he recognised that it was "not, as Plinie thought, proper to the Alps only." Camden (1610) believed the Chough was confined to Cornwall: "in the rocks underneath (St Michael's Mount), as also along the shore everywhere, breedeth the *Pyrrhocorax*, a kind of crow, with bill and feet red." However, earlier, in the mid-C15 (publ. 1651), Upton reported: "but few in number ... *most* [my italics] in Cornwall". Merrett (1666) reported the Chough's presence "on all the sea coasts from Cornwall to Dover". He was the first to give a realistic account of its distribution in Britain. In 1662, Francis Willoughby (1676) and John Ray (1678) (quoted in Penhallurick 1978) saw "great flocks" near Padstow (see Figure 2.10, Table 3.1), and followed Merrett *viz* "not only in Cornwall but also in Wales and all along the western coast of England about the cliffs and near the sea."

A century later, Gilbert White wrote to two correspondents, Barrington (1770) and Pennant (1771), "the Cornish Chough builds I know all along the chalky cliffs of the Sussex shore" and they "abound and breed on Beachey-Head and on all the cliffs of the Sussex coast". These are the first references to the Chough in Sussex, and yet Montagu (1802) was to describe it as "chiefly confined to Devonshire, Cornwall and Wales". These are reliable records: White is famous for the accuracy of his observations, and Montagu, who knew the south of England well, claimed that the Chough was "lost" from Kent and Sussex by 1802. That it was a familiar bird in the south-east is testified by the fact that it appears frequently on coats-of-arms etc., especially in Kent. Outlying remnant populations might have been overlooked but it seems certain that the Chough was extinct in these counties by 1810 (Owen 1985). This points to a dramatic decline in the last half of the C18, although, Montagu (1798, quoted in Loyd 1929) reported that it was "frequent" in S Devon "where the cliffs were high." Consistent breeding in Devon and Dorset ended pre-C20. A fairly reliable late (*ca*.1910) record exists for S Devon (Hurrell 1965), and regular breeding ceased then in N Devon (Owen 1985). Excepting Montagu's work in Devonshire and a review by Mansell-Pleydell in Dorset in 1888 (in loc. cit.), there are few reliable accounts for the remaining southern English counties. A range of books published approximately a century later, all testify to the Chough's increasing rarity (*e.g.* see Dixon 1888, Bonhote 1907, Johns 1909).

3.3 DEMOGRAPHIC TRENDS

3.3.1 CORNWALL

The Chough is now extinct in Cornwall. In Section 3.2, the background of study within the region was described; it was explained why and how this was more complete for Cornwall than elsewhere. This is now examined in a litle more detail.

Owen (1985) reviewed much of the evidence. His attempt at "systematically recreating the extent and size of a bird's population, to an acceptable degree of detail over two hundred years" relied, inevitably, on isolated and largely unquantified accounts. Many secondary sources were identified and excluded, nevertheless a high error potential remains when attempting to correlate vague estimates of bird numbers over several centuries with parameters such as age structure (admitted by Owen to be inadequately known), "potentially suitable coastline" and so-called "'ideal' conditions".

Owen attempted "To examine the geographical patterns of distributional changes against time". He constructed a population estimate based on unofficial trapping returns using a formula devised by Richford (1978) for Jackdaws. It is doubtful, however, that the data warrant such faith. The source was a remark by Bullmore (1866) that "they (Choughs) were caught in large numbers on Perran Sands .. several dozen .. annually .. throughout the game season. I have seen as many as five lying dead at one time". Owen, probably with good cause, attributes depletion of the Chough population by the 1870s to such "large-scale trapping" but assumes that from 1830 through 1850 "this level of cropping must have been a sustainable loss". This is a non-sequitor if Bullmore's discussion of animals "procured during the last six years" (in this case from one location) is not a reliable source for general application throughout Cornwall for a period of four decades (3.4.6.a-b).

Applying Bullmore's data and Richford's formula, Owen estimated a breeding density in Cornwall of 2.43prs/1 mile of coast: nearly 75% more than suggested for coastal Wales (1.79prs), and nearly double that for Ireland (1.31prs). Bardsey was estimated at 3.44prs. Converting these data to a population estimate, Owen gives:

Bardsey Island	720.5 individuals
Cornwall	508.8 "
Wales (mainland coast)	375.9 "
Ireland	274.6 "

Of these, on current census returns, only the Welsh value looks at all possible but even so the modern estimate of 381-390 individuals for Wales includes both inland and Bardsey data (Bullock *et al.* 1985).

Owen graphs the decline in Cornwall by 20 year isobars for the period 1750-1960. Cornwall receives individual attention because of the better quality of available data and geographic position: a peninsula at the toe of the country with southern and northern aspects and a long coastline (>200 miles) relative to land mass (see Section 7.3.2).

There is a pattern of linear clockwise decline (3.4.2). A Lizard record post-dating extinction farther west might be explained by the contemporary poor communications in that region; transport systems by-passed the Lizard *en route* Lands End and it remained relatively isolated with a low human population (Hopkins 1983, Bristol University 1987). If so, this strengthens the theory that the impact of human presence, influenced by outside market forces, was an important decline factor (3.4.6d-f). Prior to the Industrial Revolution (1760-1840), agriculture was a major and generally positive influence on wildlife (3.4.6e). At the turn of the C18 Cornwall, was still considered coastal and "primitive" compared to other areas of Britain, where the agricultural revolution was gaining momentum (Fraser 1794). The Cornish literature gives an impression of Chough status within the county since the C19. Table 3.1 and Figure 3.2 tabulates the chronology of all the known reliable records that I have been able to locate. Although no earlier record suggests rarity, by 1813 it was reported to have disappeared from SE Cornwall, heralding, it seems, the final decline.

Tin mining was a dominant industry until the 1860s but many workers in the industry were really miner-farmers and had been so probably since Celtic times (Bullock *et al.* 1983e). They were responsible for the patchwork of small coastal fields. Cornwall was enclosed earlier than the rest of England (Roberson & Stamp 1941), however until the early C19, dairy farming was unimportant and unenclosed sheep pasture abundant (Worgan 1811). Later in the C19, the price of tin slumped, the railway arrived and the pattern of Cornish agriculture changed radically with an increase in corn growing. Many miners emigrated and crofts, shepherding and grazed cliff pastures were abandoned. Some of the more fertile ones were amalgamated and converted to dairy farming, which the railways promoted and which boomed from 1860 onwards (Roberson & Stamp 1941).

The decline of the Chough appears to be linked in part at least to the decline in sheep-farming and the growth of dairy-farming charted by Roberson (*ibid.*). An observer, Harting, writing in 1880, believed that a rapid decline began in the 1860s and continued through the 1870s; Hart

Table 3.1 The historical record of Choughs in Cornwall. Key to localities in Figure 3.2

Period	Locality	Record	Source
1600-1700	13	present	Owen (1985)
1607	13	'all along coast'	Camden (1610)
1662	31	'great flocks'	Ray (16??)
1724	17	'great numbers'	Defoe (1768)
ca.1813	2	gone	VCH/CBRU
1816	7	'frequents', 'plentiful'	Polwhele (1816)
1816-49	14	very common	Paris (1816)
-1820	4	gone	VCH/CBRU
1832	9	gone	VCH/CBRU
1853	14	'former nest site'	Rodd (1880)
1848	6	breeding site	Johns (1848)
-1848	8	breeding site	Johns (1848)
-1849	16	gone	VCH/CBRU
1852	20	eggs collected	Rodd (1853)
1853	15	'disappeared'	Rodd (1880)
1854	12	1 nest	Clark/VCH/CBRU
1856	5	'tolerable abundance - declining to east'	Jenkins (1856)
-1856	7,10,11,14, 19,21,22,26, 31,32,34,40	'tolerable abundance'	Jenkins (1856)
1861	15	'rarely seen ... eggs much sought after'	Blight (1861)
1862-5	3	unconfirmed reports	anon.
-1863	6	extinct due to collecting	Hill (in Johns 18
1863	8	'much sought after ... eggs so prized, they will soon be extinct'	Hill (in Johns 18
1865	8	bred, robbed - 1 of 3 taken	L'Estrange (1865)
1866	23	'caught in large numbers'	Bullmore (1866)
-1870s	20	disappeared	Pk (1978)
1880	31	'impending extinction'	Rodd (1880)
1883	31	2 shot	Gatcombe (in Pk 1
1885	34	none seen	Smith (in Pk 1978
1899	18	1 shot	CBRU
1900	17	absent	Hudson (1908)
1901	28-40	7 nests recorded	Clark/VCH
1904	28-40	10 nests recorded	Pk (1978)
1905	28-40	12 nests recorded	Pk (1978)
-1920-36	29	bred most years	Ryves (1948)
1924	36,38	breeding site	Cox (in Pk 1978)
-1928	25	breeding site	Pk (1978)
-1930	35	breeding site	Pk (1978)
-1930	37	breeding site	Pk (1978)
-1930	39	breeding site	Pk (1978)
1930-38	31	bred most years	Pk (1978)
1930-44	31	breeding site	Ryves (1948)

continued ...

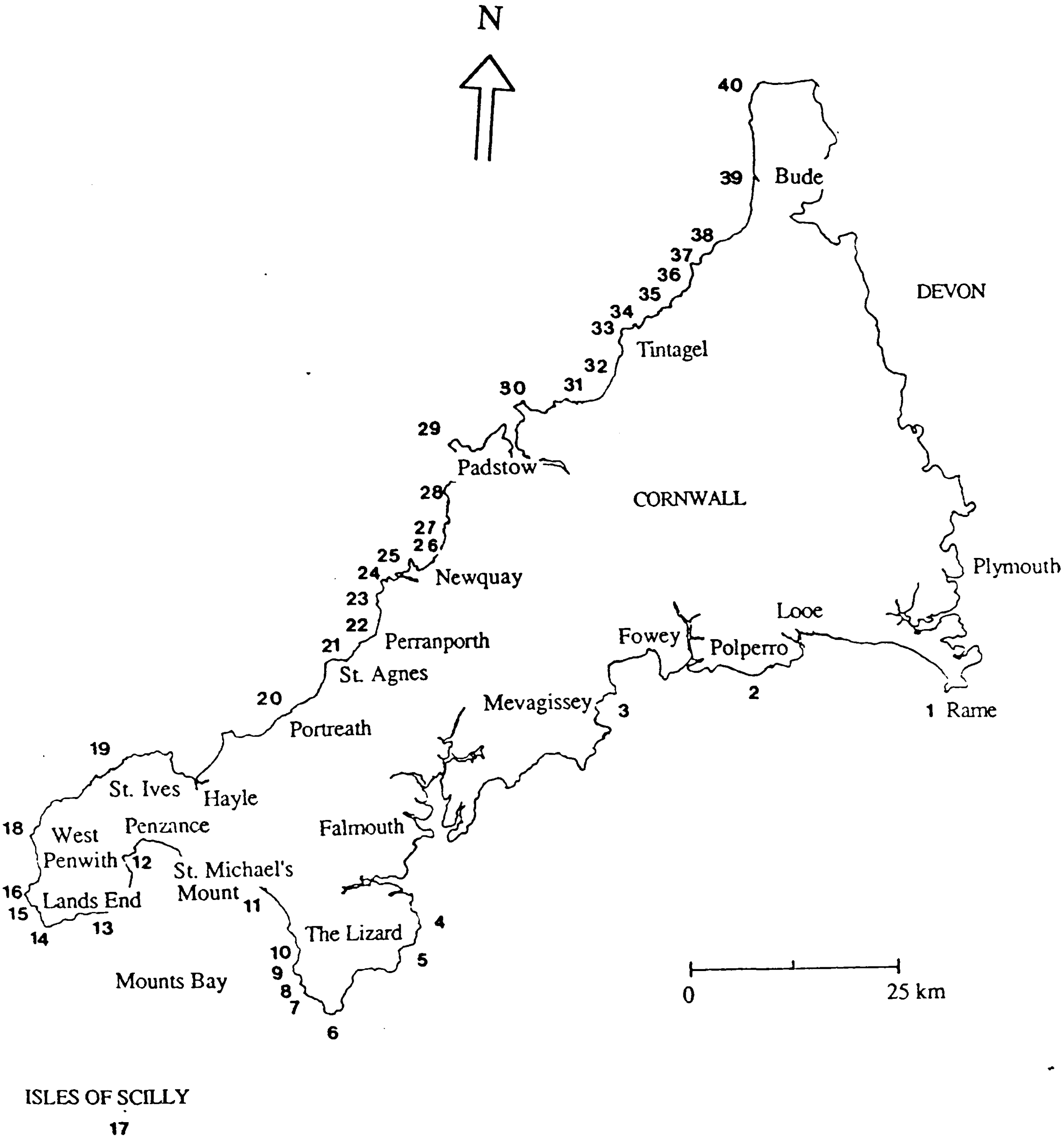
Table 3.1 continued

Period	Locality	Record	Source
-1931	32	breeding site	Ryves (in Pk 1978
-1931	34	breeding site	Pk (1978)
1931	39	deserted	Cox (in Pk 1978)
1931	1-40	<7 pairs - all 26-33	Ryves (in Pk 1978
-1932	38	gone	Cox (in Pk 1978)
1932-47	33	bred most years	Pk (1978)
1937-38	29	did not breed	Ryves (1948)
1938-47	28	young reared most years	Ryves (1948)
1939-40	24	(attempted) breeding	Ryves (1948)
1939-40	31	failed	Pk (1978)
1939-47	29	young probably reared annually	Ryves (1948)
1940	24	pair, 1 caught in trap, released with broken leg	CBRU
1941	13	*ca*.11 (3prs, 2 bred)	CBRU
1941	27	15	Hawken/CBRU
1943	31	'male (?) killed'	Pk (1978)
1944	31	3 young reared - never seen here again	Pk (1978)
-1945	25	deserted	Ryves (1948)
1945	31	'bred successfully'	CBRU
1946	27	10 (?2 broods)	Darke (1971)
1947	27-30	3/4 broods	Darke (1971)
1948-51	27-30	4 birds seen	Darke (1971)
1954	27-30	3 birds seen	Darke (1971)
1957	29	bred, young hatched?	Pk (1978)
1968	28	1 found dead	Darke (1971)
1968-73	28-29	last bird alive	various
1987	1	2 birds present	Meyer (1990)
1988	1	1 died, 1 departed	Meyer (1990)

CBRU	Cornwall Biological Records Unit
Pk	Penhallurick
VCH	Victoria History of the County of Cornwall

Figure 3.2

Locations of areas of disappearance of the Chough in Cornwall (see Table 3.1)


N
40
39
Bude
38
37
36
35
34
33
DEVON
Tintagel
32
30
31
29
Padstow
28
CORNWALL
27
26
25
24
Newquay
Plymouth
23
Looe
22
Perranporth
Fowey
21
Polperro
St. Agnes
2
Mevagissey
20
3
1 Rame
Portreath
19
St. Ives
Hayle
18
West Penwith
Penzance
Falmouth
12
St. Michael's Mount
16
Lands End
11
15
13
4
14
The Lizard
10
5
9
Mounts Bay
8
0
25 km
7
6
ISLES OF SCILLY
17

(1953) largely concurs. The profound land-use changes, in association with burgeoning human pressures, must have seriously affected the Chough. Island sanctuaries with agrarian economies, equivalent to Bardsey, Ramsey and Skomer in Wales, which might have provided valuable sanctuaries, were missing off the Cornish coast (see below and Section 7.3.2).

3.3.2 WEST WALES

The decline evident in Scotland and England (3.1.1) was apparently repeated (or continued) elsewhere in Britain. "There can be no doubt that 50 years ago [*i.e.* in the 1840s] the Chough was a common bird on the (Pembrokeshire) coast... It is now rapidly becoming scarce", so said M.A. Mathew in 1894, without unfortunately revealing his historic source. Persecution was one obvious cause, for Mathew's account largely concentrates on oological exploits (3.4.6.d); he concludes: "Apart from the persecution they meet with, the Choughs appear to be dying out in Pembrokeshire just as they are in Cornwall and Devonshire, where in former years they were equally numerous."

There is much less historical evidence than for England (=Cornwall). The lighthouse island of Caldey might encapsulate the general picture. Ebben (in loc. cit.) wrote in 1881: "The Chough breeds upon the island, and never goes away." It was 'believed' they still bred there in 1894, "they certainly did some four or five years ago", but Donovan (1972) stated "they are not proven to breed in recent years on Caldey. They are usually present there however". Bullock *et al.* (1983d) gave "possibly 1 pair", more recently, the above mentioned author and county bird recorder, Jack Donovan, has reports of two pairs of Choughs using the island in 1990 "but that only one pair is thought to have bred" (pers. comm.).

Bullock (1985) believed that the position in Pembrokeshire generally had "remained stable since 1971" and might even have slightly increased. Choughs ringed on Bardsey Island in North Wales have been reported in Ceredigion and Pembrokeshire, 100km and 160km south respectively (Roberts 1985). Ramsey Island, with as many as 9 pairs and flocks of 42 and 62 (Donovan 1972), might at times be a recruitment centre. At the time of a brief visit in July 1989, a breeding population of 3-5 pairs was estimated, a figure in line with estimates for the island during periods of low grazing pressure (Bullock *et al.* 1985; see Appendix V).

3.3.3 NORTHERN FRANCE AND THE CHANNEL ISLANDS

The Channel Islands come within French zoogeographic influence (Figure 3.1), also, because the human population is islandic with very different traditions and cultures from mainland Britain, the islands were omitted from Section 3.2. On Sark, the final nest was robbed in 1906, causing extinction; the culprit commenting that he did not understand why they were not more numerous... "I am inclined to think the Jackdaws ... may drive them away(!)" (quoted in Dobson 1952). Probable periods of actual extinction on the other islands were: Alderney 1875, Jersey *ante*1900 and Guernsey 1929 (*ibid.*).

Guermeur & Monnat (1980) and Thomas (1989) have provided good reviews of the historic Breton status. The first reference is Belon (1555). Many subsequent records in C17-20 suggest long tenure of present sites but a retraction from others. Earlier authors might have over-estimated populations due to a misunderstanding of flock structure, with sub-adults sometimes being regarded as breeding birds (Guermeur & Monnat 1980). The decline began in *ca*.1820 with "a sharp fall" occurring over the following 60 years with the species finally disappearing from Cotentin *a*1870 and Pays de Caux in 1870-80 (*ibid.*, Yeatman 1976) in west and east Normandy respectively. Vagrants were occasionally seen or captured at Cotentin until 1913 (Geurmeur & Monnat 1980). In southern Brittany, on two islands located either side of Belle Ile, a nest site identified on Houat in 1850 (Delalande 1850 in loc. cit.) was unused by 1868 (Mayaud 1933 in loc. cit.), and on Groix, where it was common in 1636 (Dubuisson-Aubenay 1898) it had gone *a*1872 (Mayaud 1933). Similarly, on the island of Ouessant, Clarke saw none in 9 days of 'careful observation' in 1898, whereas *ca*.40 had been seen 18 years before; they returned in 1933 (Guermeur & Monnat 1980). Indeed, a revival seemed to occur: in the 1950s, they were reported as being "numerous in all their traditional haunts", however it is possible that the underlying trend was still downwards (*ibid.*).

On Belle-Ile, "formerly the best haunt" (Thomas 1989) of Breton Choughs, in the mid-1950s, Kowalaski (in Guermeur & Monnat 1980) twice estimated the number of pairs at *ca*.40, but in 1973 and 1974 only 10-15 pairs are recorded (Thomas 1989) and the maximum flock size had reduced from 56 in 1949 (Moreau & Moreau 1959, in Guermeur & Monnat 1980), 80-100 in 1952 (Burnier & Burnier 1969 in loc. cit.) and 50 in 1957 (Kowalski 1957 in loc. cit.) to 36 in 1970 and 22 in 1971. On Cap Sizun and the Crozon peninsula, the same pattern applied: on 25km of the Leon coast, 6 pairs in 1965-69 declined to only one in 1975 (*ibid.*). Only on Ouessant did the situation show any improvement: 6 pairs in 1969 (A. Thomas unpubl. data) increased to 10 pairs in 1973. Flock sizes fluctuated from 10 (1948) to 65 (1966) to 17 (1971); they then showed some increase: to 29 in 1973 (Guermeur & Monnat 1980).

In conclusion, the total breeding population for Brittany was estimated at 30-45 pairs in 1973 (*ibid.*). Synchronously with the major British and Irish survey in 1982 (Bullock *et al.* 1983a), the *Societe pour l'Etude et la Protection de la Nature en Bretagne* (SEPNB) surveyed Brittany and estimated 23-35 pairs, with some previously occupied territories vacant. Subsequent work in 1987-88 gave an estimate of 28-37 pairs, suggesting either that the earlier estimate was low or that the decline has been arrested (Thomas 1989).

3.4 FACTORS CONTRIBUTING TO DECLINE

3.4.1 INTRODUCTION

Rolfe (1966), in one of the first assessments of the decline, stated: "There seems to have been several causes, not one of which stands out as generally applicable". He identified *human persecution*, *natural predators*, *jackdaws*, *climatic influences*, *inbreeding and disease*, and *toxic chemicals*. In this study, five major parameters have been identified (Table 3.2); all Rolfe's criteria are covered within these, the last mentioned under 'Changes in land use'. This chapter takes each of these variables in turn, and building on Rolfe's conclusions, reviews their possible effects during C19-20 on the present status and distribution. Table 3.1 clearly shows that the decline was gradual, and not the result of sudden events, although these might have affected on-going trends.

Table 3.2 Possible factors influencing decline of the Chough

1 CLIMATIC
2 GENETIC DEPRESSION
3 DISEASE
4 PREDATION
5 INTERSPECIFIC COMPETITION
6 HUMAN INTERFERENCE :
  a) Shooting and intentional killing
  b) Trapping for captivity
  c) Accidental trapping
  d) Egg collecting
  e) Changes in land use
  f) Impact of presence - repercussive disturbance etc.

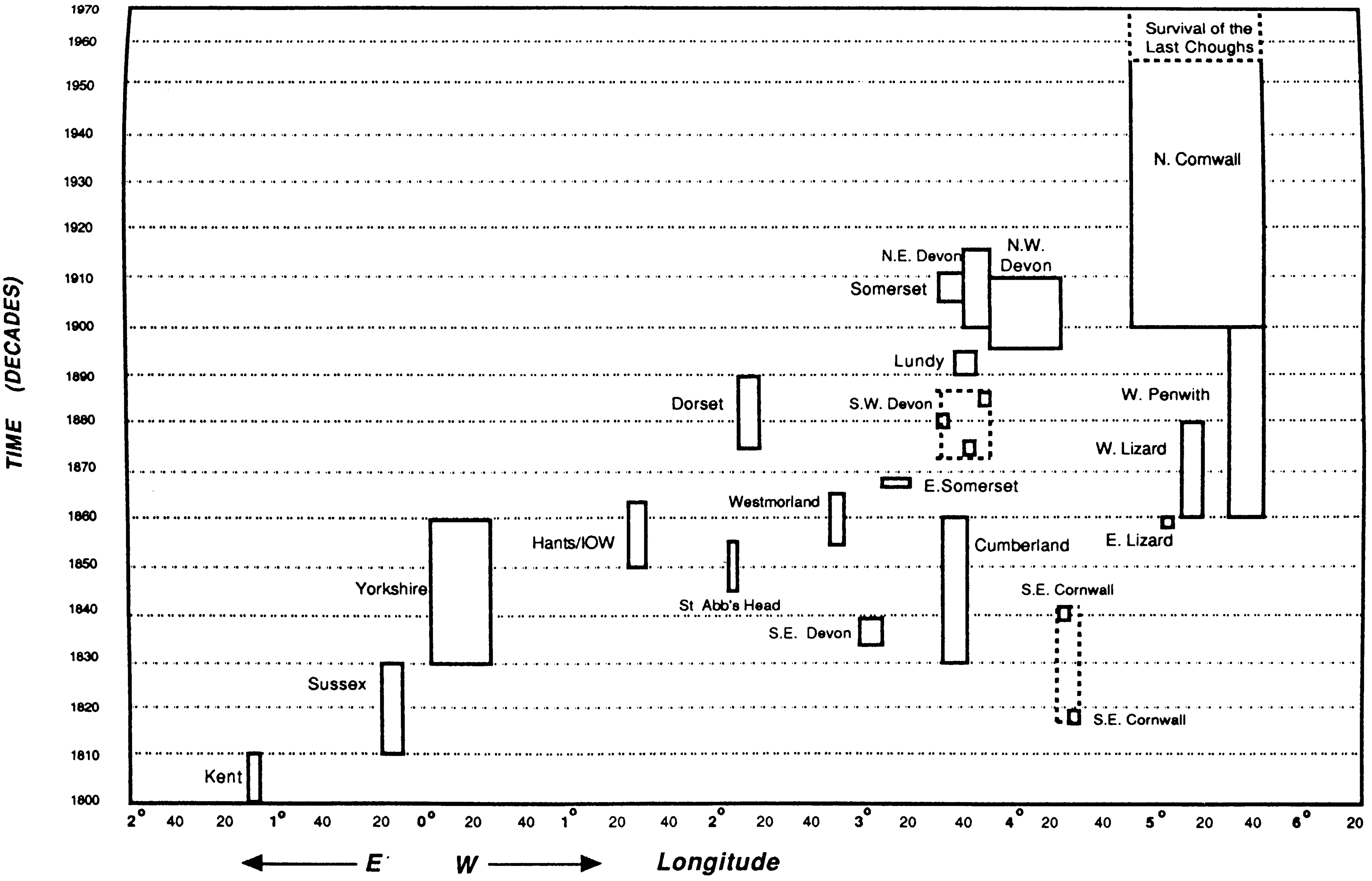
3.4.2 CLIMATIC EFFECTS

Rolfe (1966), Bullock *et al.* (1983a) and Monaghan *et al.* (1989) discussed broad weather patterns. Mean annual temperatures in Britain decrease from SW to NE; areas exposed to the Atlantic oceanic influence have the highest annual means (a result of mild winters) as opposed to those more affected by the continental influence (Chandler & Gregory 1976). The southern coastal parts of Ireland, Dyfed and the West Country are the only areas with a mean January temperature of $>5^{o}$, which may be regarded as the threshold temperature over which accelerated growth of vegetation occurs (*ibid.*). The 4° January isotherm shows that the extreme west of Scotland is as warm as the south coast of England eastwards from the Isle of Wight (*ibid.*). Cullen & Jennings (1986) demonstrated the high correlation of Chough distribution and the equivalent Fahrenheit isotherm (38°).

Bullock *et al.* (1983a) plotted the chronology of the Chough's decline by region. Owen (1985) reviewed the historical record more critically and rejected secondary and unreliable sources. These data are reassessed, some additional records included, and plotted against longitude (Figure

Figure 3.3

The decline of the Chough in England measured by longitude. X axis: length of coastline in degrees longitude; Y axis: known dates of last records

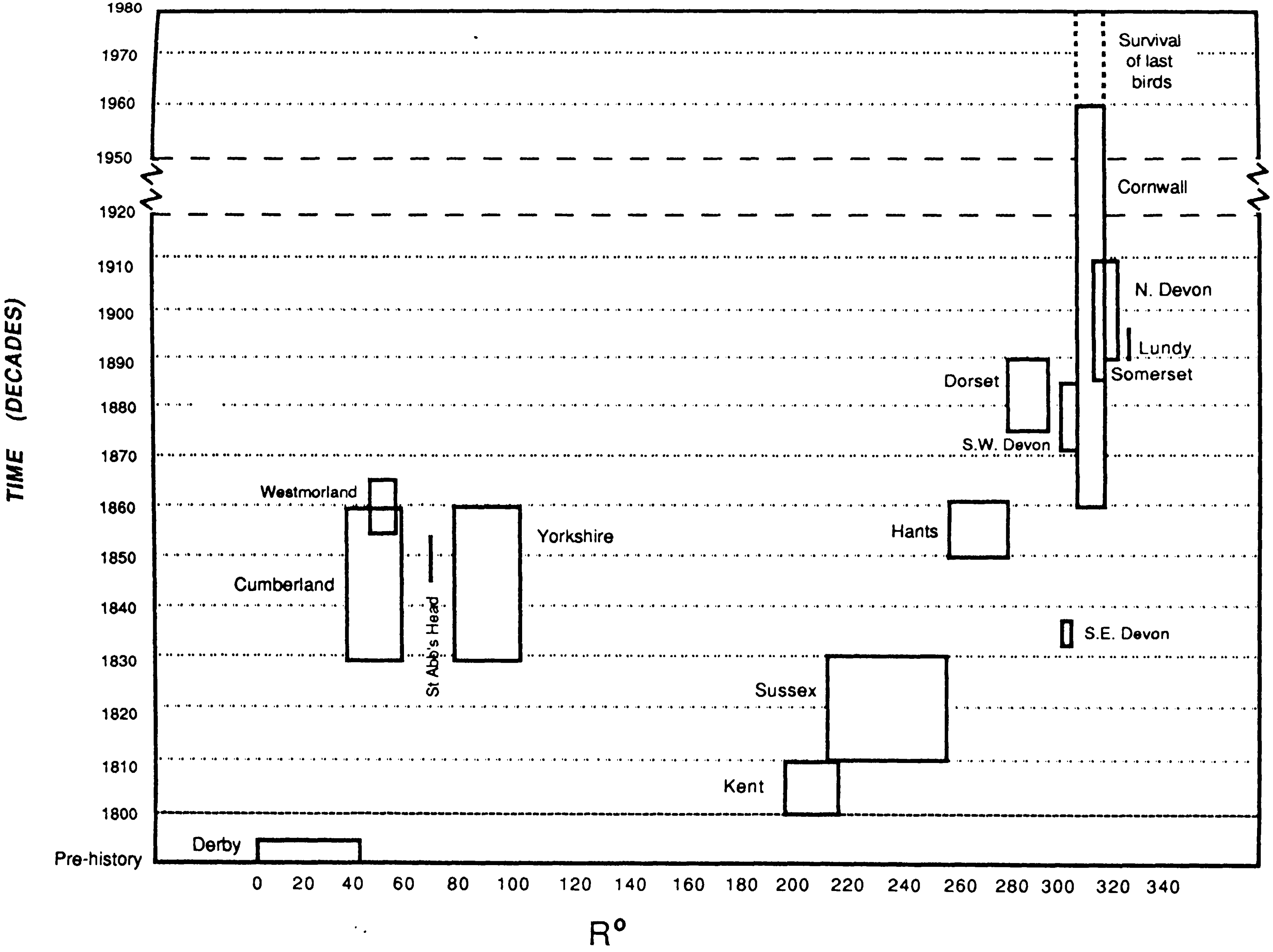

TIME (DECADES)
1970
1960
1950
1940
1930
1920
1910
1900
1890
1880
1870
1860
1850
1840
1830
1820
1810
1800
Survival of the Last Choughs
N. Cornwall
N.E. Devon
N.W. Devon
Somerset
Lundy
W. Penwith
Dorset
S.W. Devon
W. Lizard
E.Somerset
Westmorland
Hants/IOW
Cumberland
E. Lizard
Yorkshire
St Abb's Head
S.E. Cornwall
S.E. Devon
Sussex
S.E. Cornwall
Kent
2°
40
20
1°
40
20
0°
20
40
1°
20
40
2°
20
40
3°
20
40
4°
20
40
5°
20
40
6°
20
E
W
Longitude

3.3). A progressive E→ W retraction is shown, which was not apparent from Bullock's review or revealed by Owen. The correlation responds largely to western oceanicity, and disregards other bioclimatic variables. Mean temperature declines → NE in Britain, and if this is taken as a more meaningful basis on which to assess habitat suitability for Choughs, north-easterly inland districts would be less suitable than the eastern coast, and sub-optimality for the Chough in Britain would begin here and radiate progressively 'clockwise' around the coast. Thus, a retraction, if one were to be induced by a general climatic change, might have been expected to have begun in central (*i.e.* away from the coast) northern districts of the Chough's known range (Derbyshire or central Scotland?) and spread southwards round the east coast of Britain, then westwards to Cornwall. Figure 3.4 re-plots the decline data by such a R^o index, which uses a theoretical central point in Britain (Northampton) as the base from which the final disappearances on County coastlines are measured in radial degrees: the 180° midline running approximately NNW through the spine of Britain.

Presumably, any effect to be identified as affecting Chough status must agree with a regional and sequential pattern of decline similar to this. Global phenomena would show national effects or exacerbate prevailing regional ones. For example, a strengthening westerly wind pattern from 1880>1920 (Rolfe 1966, Chandler & Gregory 1976) cannot be a root cause of a decline that began in eastern districts early in C19 (Figure 3.3). A series of cold winters, with temperature ***minima*** mainly during 1837-55 and 1878-98, could have affected status, either by affecting food supply or increasing susceptibility to human persecution (3.4.6), but by then Chough decline was already in progress. Until 1940, the pattern ameliorated, with a warming of *ca*.2.8^o: an improvement in Chough numbers might

Figure 3.4

The decline of the Chough in England measured by clockwise radial linearity (see text). X axis: length of coastline as represented by R^{o} from a theorised central point within the British landmass (*i.e.* Northampton); Y axis: known dates of last records


TIME (DECADES)
1980
1970
1960
1950
1920
1910
1900
1890
1880
1870
1860
1850
1840
1830
1820
1810
1800
Pre-history
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
320
340
R°
Survival of last birds
Cornwall
N. Devon
Lundy
Somerset
Dorset
S.W. Devon
Hants
S.E. Devon
Sussex
Kent
Westmorland
Cumberland
St Abb's Head
Yorkshire
Derby

have been expected but no such improvement is evident, unless by this time other factors had taken effect. The period 1740-1810 gave a consistently high level of summer temperatures (*ibid.*). Rolfe's 1963 survey, undertaken immediately after the severest winter in living memory, found little evidence to suggest a consequential decline. There was certainly individual hardship and some deaths, evidenced by distressed Choughs feeding in streets and gardens but no widespread mortality. However, such observations and a recent study (Meyer 1990, see Appendix IV), show that severe weather does change behaviour patterns. An account from an experienced naturalist-farmer in West Wales suggests possible longer-term results:

> "We had 2 particularly severe winters, consecutively, 4 or 5 years ago, the low temperatures made worse by almost continuously northerly winds. This killed the exposed Gorse bushes, and I think must have penetrated so deeply as to kill most of the ants. It has certainly changed the summer feeding of the Choughs at Ceibwr [adjacent and S of Study Area W1 (2.3.2, see Figure 2.6c)]. One could almost guarantee them feeding on the rough meadow ... covered with ant mounds, - now they are seldom there, though close grazing by ponies and rabbits is maintained" (M. Patterson 1988, pers. comm. to NCC, Dyfed-Powys).

3.4.3 GENETIC DEPRESSION

The Chough is a sparsely distributed sedentary species which breeds in isolated pairs within isolated (or patchy) communities (Rolfe 1966, Coombs 1978, Monaghan 1989). If outbreeding maintains genetic variability, which is valuable when adaptability to a changing environment is needed (O'Connor 1985), it would appear, at first sight, to be a candidate for inbreeding depression through high homozygosity. Malan (1891) was possibly the first to discuss inbreeding in reference to Choughs, stating "there would be fewer opportunities for the survivors to find fresh alliances in the way of mates..." after numbers had been reduced by human persecution and competition from Jackdaws. Malan advocated the introduction of new blood, and as a result, one JP Woods, a Fellow of the Zoological Society and manager of zinc mines in Spain, offered to catch "any number of red-legged choughs, entirely free of cost, to turn loose on the Cornish cliffs". Fortunately (or unfortunately) the promise was not fulfilled due to problems encountered in keeping adult birds alive and, afterwards, the hand-reared nestlings died during Mr Woods' absence.

There is no evidence to suggest that the species has ever been densely distributed in Britain, and the expectation would be that when populations are chronically reduced and isolated, inbreeding depression would occur (Frankel & Soule 1981); however, this, could not *ipso facto* be a primary cause of decline but rather a consequence of it. In Brittany, where the Chough has been isolated at a low level since at least the 1940s and possibly much longer, there is no evidence that any diminished heterozygosity has affected reproductive success (3.3.3). Examination of isoenzyme variation on Islay suggests that the genetic variation on this island is in the middle to upper range of values when compared to a large number of bird species, and that the Chough on Islay has not suffered a loss of genetic variability (Monaghan 1989). Elsewhere, the rate of decline might well have outpaced genetic effects.

3.4.4 DISEASE

There are insufficient data to assess the role of disease as a limiting factor on Chough status (Bullock 1980). Two diseases have been recorded:

pseudotuberculosis and gapeworm. The former is a bacteriological disease caused by the pathogen *Yersinia pseudotuberculosis*, and is seen mainly in the winter when animals are in sub-optimum condition due to climatic and environmental effects (Petrak 1969) although Cowdy (1962) reports a female Chough dying on her nest from the disease on Bardsey in 1958; she also refers to other recent deaths of nestlings and fledglings from unknown causes. Rolfe (1966) quotes similar evidence from Merionethshire. Pseudotuberculosis is seen in predators which have eaten infected prey, and in all animals which have taken contaminated food (Petrak 1969).

The Gapeworm is a blood-sucking nematode *Syngamus trachea* that infects the trachea of many species of birds. The worms cause considerable irritation to the lining of the trachea, and can obstruct the airways. Eggs are coughed up, swallowed, and are voided. Usually the eggs hatch to produce larvae which are ingested by invertebrates such as earthworms (Lumbricidae), where they become encysted and can remain for months or years (Meyer & Simpson 1988, see Appendix VII). Birds which eat the infected prey (or the eggs themselves (Cox 1968)) can then become infected.

It is likely that the lame birds occasionally reported, including from Cornwall (Ryves 1948) are suffering from the *Yersinia* bacterium. Recently there has been more discussion about gapeworm, but a century ago, in 1891, Malan remarked of Choughs in captivity needing 'absolute liberty and full exercise of wings; if not, they generally developed asthma in their first year, which usually proved fatal.' 'Asthma' might well have been gapeworm since the wheezing symptoms could easily be confused; gapeworm is a common disease of many captive birds, especially juveniles (Wilkinson 1987). It has been recorded in wild Choughs from the Isle of

Man (Haycock 1975), Scotland (Bignal *et al.* 1987), Cornwall (Meyer & Simpson 1988, see Appendix VII); and very recently from an adult found dead at Marloes (Study Area W4) (R. Haycock & V. Simpson pers. comm's.), the first record I have from Wales. Gapeworm is known to affect the Magpie and Carrion crow ((Meyer & Simpson 1988, see Appendix VII), the Rook to a considerable extent (Holyoak 1971, Barus *et al.* 1972) and Starling (Lapage 1956).

It has been suggested (Bignal *et al.* 1987) that relatively small and isolated Chough populations might be vulnerable to outbreaks of chronic gapeworm infection, particularly nestlings if the parents are collecting food from an infected area, or concentrating on a particular type of food such as earthworms, if heavily infected. Meyer and Simpson (1988, see Appendix VII) noted that parasitic infections normally only become significant when the host is under stress, possibly from intercurrent disease or malnutrition, or where the challenge is very high, *i.e.* in captivity, which is virtually what Bignal *et al.* are suggesting. If the environment is being contaminated by other corvids or Starlings, which are themselves not affected, there are obvious dangers to less resistant predators or less experienced and stressed birds. Brown & Thompson (1986) suggested that dominant Golden plovers and Lapwings can identify infected prey, but the situation may be envisaged where stressed birds, perhaps when feeding young under difficulties, breeding for the first time, or when pioneering in unknown areas (=less experienced), could be as at risk as subordinate birds (Meyer & Simpson 1988, see Appendix VII). Resistance to gapeworm could be impaired by malnutrition-induced stress, and Choughs feeding sub-optimally, due to insufficient optimal or degraded habitat, could be at increased risk from gapeworm (*ibid.*). In conclusion, disease is unlikely to have been a primary factor but may have been a secondary element, and could also be inhibitory to recolonisation.

3.4.5 INTERSPECIFIC RELATIONS

3.4.5a Predation

The Chough has few avian predators (Rolfe 1966). Bonhote (1907) claimed the Peregrine "will attack it, resulting in very rapid extermination", and it has, more recently, been implicated in some local declines, *e.g.* Islay and other Scottish islands (Baxter & Rintoul 1953); but although remains are occasionally found at eyries, it is extremely doubtful if this predator has affected the status of the Chough in Britain (Ratcliffe 1980). Cade (1960) believes that the Peregrine is a good example of the basic Errington hypothesis: *i.e.* vertebrate predators live on the expendable *surpluses* of their prey populations. There are records of Peregrines taking Choughs in Pembrokeshire but only 3 in 20 years of observation (Gilbert 1927), and one in Snowdonia (Ratcliffe 1980). The skull in Figure 1.3 was from a Peregrine plucking site at Strumble collected by R. Spicer. It is possible that a Peregrine accounted for one of the last 'true' Cornish Choughs (Penhallurick 1978). I twice saw a Peregrine stoop unsuccessfully at Choughs which had returned to Cornwall after an absence of 20 years, and it is probable that, when very sick from the affects of gapeworm (3.4.4), a Peregrine finally succeeded in catching one (see Appendix IV).

Bonhote allowed that the 2 species could co-exist peacefully, and Ryves (1948) describes such at all the sites he knew in Cornwall. Peregrines and the larger corvids can, though, cause disturbance (3.4.5 and 6.3.3).

In Pembrokeshire (Study Area W1: Mwnt-Cemaes), no direct attacks were witnessed but on one cliff where they nested about 100m apart, a Peregrine would often indulge in mock or redirected attacks, as described by Ratcliffe (1980) in relation to Ravens, during nest visits by Choughs, causing considerable alarm. This nest failed to produce young in 1988 but did the following year when the Choughs moved a short distance away out of sight around a headland.

Rolfe (1966) cites possible predation of nesting or young Choughs by Little owls, Hooded crows, Foxes and rats, but these cannot be significant given the usual inaccessibility of Choughs' nest-sites (Bullock 1980). Warnes (1985) also cites rats, and adds ferrets and feral cats as possible predators of nests on Islay; rats have also been known to raid nests on the Calf of Man.

3.4.5b Competition

The Jackdaw is the species which has generated most comment with regard to Chough status. In the early literature the Jackdaw is frequently cited as being a major cause in the decline of the Chough (see, *e.g.* Gray 1871, Bonhote 1907). Gray wrote:

> "In almost every district I have visited of late years, jackdaws have increased to an excessive extent; and until some other and more satisfactory explanation be given for the Chough's absence, the increase of one bird, I suspect, must be looked upon as the cause of the decrease of the other."

Rolfe (1966) stated: "Older writers, almost to a man, held the Jackdaw responsible ... assuming a simple equation between the increase of the one species and the decline of the other". Stewart (1928) expressed the conundrum, probably drawing on Buchanan (1882):

> "Nearly all accounts seem to agree that everywhere the places it (the Chough) once frequented or now tenants in diminishing numbers, swarm the ubiquitous Jackdaw, and strange to relate it is everywhere said to live on the friendliest terms with that bird."

The role of the Jackdaw was diminished by Ryves (1948) and more recent authors, though it is still heard frequently from the layperson, and given credence by some, *e.g.* Dobson (1952), Guichard (1962) and Yeatman (1971). Darke (1971) suggests reasonably that competition might occur at times. He recognised that the Jackdaw prefers insect food when available (see Coombs 1978), and cites the following personal observation:

> "a field of barley which failed as a result of depredations by wireworm was resown in late May, at a time when the jackdaws were feeding their nestlings on the cliffs. Immediately after drilling, while the earth was still disturbed, a horde of jackdaws settled on the field and attended it until the corn was showing well above ground ... [the Jackdaws were thought to be eating the corn, but] ... when one was shot, its crop was found to be full of wireworm (the larvae of elaterid click beetles) ... the birds were probably instrumental in saving the corn."

Darke suggests that where Choughs and Jackdaws are rearing young in close proximity, some competition for insect larvae seems inevitable. Goodwin (1986) accepts that where Jackdaws and Rooks are absent or restricted, the Chough could exploit a wider range of feeding places. Dory (1983, 1989) argues against Jackdaw involvement by referring to the situation in the European Peaks, particularly the Cantabrican mountains and the Covadonga National Park, Asturias, which has seen a dramatic reduction in Chough numbers "Only 20 years ago, flocks of hundreds ... were commonly seen in the low valleys during winter, now they are hardly ever seen. In the same way, the presence [on the coast] mixed with gulls in some places, is something that has disappeared almost completely". The Jackdaw, while increasing on the Continent in the last decades, is not present in Cantabrica, "so that possibility can be ruled out" (Dory 1983).

Jackdaws did increase synchronously with a Chough decrease between 1830 and 1890 but the Chough decline had begun somewhat earlier (3.2). It is perhaps more likely that alterations in habitat quality, caused by human activity (3.4.6e), have affected it to the benefit of the Jackdaw and the detriment of the Chough independently.

In the few Chough/Jackdaw interactions noted during the present study, Choughs were the instigators. There were also territorial disputes between Choughs and other sympatric corvids in which this was not necessarily the case (see Section 6.3.3) but with the possible exception of competition between Choughs and Rooks for leatherjackets (*Tipula* spp. larvae) and wireworms (Elateridae larvae) on old pasture, there seemed little overlap in niche partitioning.

3.4.6 HUMAN INTERFERENCE

3.4.6a Shooting and intentional killing

Rolfe (1966) gives shooting as an important pressure. Choughs have been hunted in substantial numbers, like any other large bird which has come into association with man. As a crow it has perhaps been killed more than most, sportsmen and farmers not discriminating on the finer points of comparative corvid ecology. Rolfe (*ibid.*) and Goodwin (1986) suggest that their relative tameness could have increased the toll *cf.* other corvids. Couch (1838) remarked that the decline was "a circumstance chiefly owing to the persecution it suffers at the hand of the sportsman, and those who supply Naturalists with specimens..." In 1827, on the Isle of Man, Jardine (1838-43) "procured nearly thirty specimens in a fore-noon." The purposeful slaughter explained by sport and pest control was compounded by casual slaughter such as displayed in the account from Braunton in Devonshire of 6 being killed on "a manure heap" from one blast by a sportsman wishing to discharge his muzzle-loader. Generally, a mix of motives pertained, as shown by the fate 4 of 6 nests on the east Manx coast in 1939: (i) 3 young stoned to death in the nest, (ii) 4 possibly taken for cage-bird show, (iii) 2 reared but shot within 8 weeks, (iv) 1 taken prior to fledging (Williamson 1959).

In Cornwall, the inherent interest in the species added to the toll: many historical records are a result of shootings. Three of only 4 Choughs recorded on the Isles of Scilly between 1870 and 1901 were shot (Penhallurick 1978). Coombs (1978), Bullock (1980), and Thomas (pers. comm.) in France, indicate that shooting still occurs in modern times.

Birds were also trapped for taxidermy, notably in Victorian times (many survive today in museums, businesses and private houses), their skins and even for meat (3.3.1). Bullmore (1866) refers to "large numbers" being caught in baited (it is not known with what) steel traps: "several dozen are sent annually to Falmouth". In the Royal Cornwall Gazette (RCG) (16.v.1870), a pair was priced at £3.10s.0d. Owen (1985) blamed such "large-scale trapping" partly for the decline of the Cornish Chough, and Penhallurick (1978), citing an advertisement in the RCG (23.vii.1891) for their capture, says "There is ample evidence that the main reason - perhaps the only significant cause (of its decline) ... has been its persecution by the very men who so revered it as their national bird."

Before the war (presumably II), a single Chough in good feather was worth £5 alive or dead (Palmer 1950s, undated pamphlet, *The Old Cornwall Society*).

3.4.6b Trapping for captivity

In Cornwall the Chough has been intentionally live-trapped and hand-reared since at least the C16 (Carew 1602). Subsequent authors have testified similarly, *e.g.* in Cornwall, Camden (1610), Borlase (1758), Montagu (1802), Edmonds (1862), L'Estrange (1865), Rodd (1880) and, in Pembrokeshire, Mathew (1894). It was "very common to see tame ones in their (Cornish) gardens" (Maton 1797). That the Chough had a role as a status symbol, both by its regular appearance as an heraldic device (3.2), and by the fact that Carew in the C16 and Borlase in the C18 often made gifts of them to eminent personages, including two young ones to the Chancellor of the Exchequer in 1757, there can be no doubt.

Choughs, in common with other corvids, make long-lived and endearing pets when hand-reared and were often tamed (Beckerlegge 1972). One at Padstow Bird Gardens in Cornwall was still very healthy at more than 22 years old in 1991. Borlase himself had one still alive at 14 years old in 1763 (Pool 1966, quoted in Penhallurick 1978); he described the species as "very amusing when kept tame; [being] docile, regular and constant to its hour for meat" (1758). Quarrymen in N Wales traditionally took one or two (but not all) from nests each year for competitive bird-showing (S. Latchford pers. comm.). In Cornwall, Malan (1891) had several Choughs and recorded that they attempted nest building but did not lay eggs. A small flock kept in a garden in Exeter had been reared from young taken in S. Cornwall (D'Urban & Matthew 1895), these are the skins now in Exeter

Museum (Loyd 1929). Many young birds acquired on nest-robbing missions were reared and kept either as pets or for sale (see Section 3.4.6a). The majority of those seen until quite recently in cage bird shows were presumably obtained thus. These have now formed the founder stock of the current captive-breeding programme (see Chapter 7).

3.4.6c Accidental trapping

Many Choughs were trapped accidentally on cliffs in the early 1900s (Ryves 1948). The cliffs were, in places, so "thoroughly sown with open gins to trap rabbits", that the decline was attributed to this (Cox, quoted in Penhallurick 1978). It is not possible to quantify this or relate it to intentional trapping (3.4.6a-b). Some were released or cared for by the trappers (Darke 1971). Chenoweth (in loc. cit.) describes how between Newquay and Perran Sands in the war years "trappers tilled their traps in the open near the cliffs ... often caught them"; he maintained this was one of the causes of their disappearance. They cannot have been common even then because one trapper at least did not recognise the species. Ian Bullock believes a corpse he found with a smashed leg in Ireland in 1979 met a similar fate (Bullock *et al.* 1983a).

3.4.6d Egg collecting

Despite often inaccessible nest sites, trade in Chough eggs flourished in the C19, and eggs are still taken illegally from Wales (Bullock *et al.* 1983a, R. Meyer unpubl. data). Eggs were used as a source of food in the Isle of Man in historic times (Cullen & Jennings 1986). In Pembrokeshire, towards the end of the C19, it was "rapidly becoming scarce, and were it not for its sagacity in building in holes and crannies of inaccessible cliffs, it would long ago have been exterminated, as all its eggs would have been taken to meet the demands of collectors" (Mathew 1894). S.W. Jenkin writing in *The Naturalist* (1856) remarked "they would ere this have been exterminated"; also "the egg of this bird is much sought after" (Blight 1861); and "they were so much sought after, and the eggs so prized, they will soon be extinct" (Hill, in Johns 1863). Darke (1971) summarised the Cornish view: "Egg collectors from England played a large part ... as they had always done, offering the near poverty-stricken working man relatively large sums... Many of these men were hardened wreckers, used to recovering the great spars and hatch covers [from] the rocks ..." In *ca*.1900, a clutch of eggs earned a retired wrecker £1 (*ibid.*). Eggs taken from Berry Head in Devonshire in 1880, one of the last breeding attempts in the county, are lodged in Torquay Museum (Loyd 1929).

3.4.6e Changes in land-use

Changing land-use as a cause of Chough decline was not appreciated until 15 years after Rolfe's (1966) survey. The importance of low-intensity pastoral agricultural systems was largely ignored, despite earlier clues, *e.g.* Whittaker (1947), Holyoak (1967, 1972), Donovan (1972), Cowdy (1973) and Gatehouse & Morgan (1973), until Bullock's work in the late 1970s (2.1; and see, *e.g.* Bullock 1980; Roberts 1982, 1983; Warnes 1982; and Bignal & Curtis 1989). Use of the land changes in direct and obvious, and indirect and subtle ways, affecting virtually all British mainland wildlife, even the Chough, which used to be regarded as a denizen of only the '*wild*' and rocky fringes of Britain (3.2). However, human use of the land substantially affects the Chough; such effects are an integral part of this study. Comments here are, therefore, confined to those of an introductory and background nature.

Man can affect Chough habitat in 2 ways: (i) by creating or removing it, and (ii) by managing it (Owen 1985). Most important are the effects upon invertebrate communities and their accessibility to the birds. For example, low-intensity pastoral systems, where invertebrate communities are not destroyed by ploughing or biocides are crucial (Curtis *et al.* 1989), as are close-cropped open swards (Bullock 1980) with earth-exposures (see Chapter 4). Occasional and selective 'cool' burning also creates open vegetation and bare earth (Haycock & Bullock 1982). Until very recently 'swaling' (controlled burning notably of 'furze') was a common winter activity on the clifflands of Cornwall and West Wales (F. Ansell & E. Latter pers. comm's.); it is still widely practised today in some parts, notably Islay (E. Bignal pers. comm.). "'Furze' is ... gorse which was harvested in faggots and used as a source of quick-heat... Furze-shoots formed a useful first-bite for stock in spring-time and farmers would not have wasted this valuable grazing resource" (Herring 1987). Burning by humans has, since *ca.*3000BC, profoundly affected the landscape, and is one of the oldest management techniques known to man. In the West Country after the onset of the wet, oceanic post-glacial phase, burning was responsible for all the extensive clearances (Balchin 1983). Cornwall, never since well-wooded, was described in 1542 as "a pore and very barren countrey of al maner of thing, except Tyn and Fysshe." A contemporary poet wrote:

> *O Cornwall! wretched spot of barren ground,*
> *Where hardly aught but rocks and furze is found...*

As stated (3.3.1), even by contemporary C18 standards, Cornish agriculture was considered coastal and "primitive" (Fraser 1794). However, a primitively farmed, poor and barren coastal landscape with rocks, furze

(*Ulex*), tin mines and attendant mules and pit ponies (=rough grazing) (see 3.4.6f) might suit a Chough very well (see Chapter 4).

The decline of tin mining perhaps more than any other single factor changed the face of Cornwall's coastal landscape. The engine houses and some of the shafts and adits still remain, now the nestsites of Jackdaws not Choughs, but the effects of the extensive rough grazing associated with this form of primitive mining has disappeared; Ratcliffe (1980; see Section 1.3.2) has described these effects. When functioning at its prime, the industry affected the landscape in two major ways: (i) the miner-farmers, enclosed much of the waste land into small squarish cliff-top fields which reached right down the cliffslopes almost to sea level, as in West Penwith (Russell 1971); and (ii) by the laying waste of much farmland (Balchin 1983). A depression in 1830-50 caused many thousands of miners to emigrate to Australia, America and Canada; a brief upsurge was followed by another depression during the American Civil War, in turn followed by the great boom of 1870-72 - which represented the all-time high of the industry: 26,500 people employed in 230 mines. However, this was followed by 50 years of depression and by 1921 only one active mine remained (*ibid.*); World War II saw a brief resurgence but with only a few mines reopened. Virtually all are now closed.

Ploughing up of coastal heaths, intensification of arable farming, retraction of grazing, and the advance of industry and other human developments, all act in visible ways which are quantifiable to some extent (4.6.3). The more subtle effects of human activity upon the countryside are likely to be of chemical origin and may require closer scrutiny to detect, *e.g.* the treatment of crops against animal and plant diseases, and the application of nitrogenous fertilizers. Compare the emerald green acres of improved monotypic rye-grass with old, permanent or unimproved pasture. The latter looks *untidy*, and is characterised by >5-10 herb species/square metre. If such unimproved pasture receives reasonably heavy grazing, or sufficient exposure such as on clifftops, a tight herb-rich sward, rich in invertebrate fauna, *e.g.* ants, Coleoptera and Diptera (staple Chough prey; see Chapter 5) is also likely to be present. As grazing pressure reduces, there is a proportionate increase in vegetation height and decrease in viability to Choughs (Bullock & del-Nevo 1983, Roberts 1983, Williams 1989, Mitchley 1990). Rotational pasture is used by Choughs on Islay (Bignal *et al.* 1988, C. McKay pers. comm. *cf.* 4.3.3) where the resource is likely to be dung invertebrates, provided these have not been precluded by the use of antiparasitic drugs such as 'Ivermectin' (McCracken 1989) and tipulid larvae.

The use of sheep-wool by Choughs as a nest-lining is well-known (Williamson 1959, Holyoak 1972); samples collected from nesting areas during the breeding season were analysed in order to investigate the possibility of chicks being affected by chemical residues within the nest (Appendix III).

3.4.6f **Impact of human presence**

To what extent did an indigenous and expanding human population, with increasing mobility and leisure-time, and a modernising post-Industrial Revolution agriculture, affect the clockwise pattern of decline plotted in Figure 3.4? The current western distribution has been given (1.3.2; see also Section 3.3.2), and the importance of islands is discussed (7.3.2), but did Cornwall become the last English refuge of the Chough largely on account of its bioclimate and geography (a large peninsula =quasi-island) or also because of its remoteness from 'civilisation?'

This section examines the repercussions of human presence on the Chough.

E. Bignal (unpubl.), discussing a proposed development on a remote part of the Inner Hebridean island of Islay (a Chough stronghold, possibly analogous to Cornwall during the C18-19), wrote:

> "The physical developments (buildings and roads) and the impact of people, vehicles and activities will introduce noise and disturbance, and thereby directly and indirectly erode the value of the area... (it) will affect breeding choughs by generating direct nest disturbance at breeding sites, resulting in incubating parents being kept away from eggs or young for prolonged periods so that the clutch or brood chills and dies. Breeding performance and therefore recruitment to the population will decline".

During times of no disturbance at one nest, in a farm outbuilding, visits by the parents to the nest were on average every 28.2 minutes (2.1 visit/hour), during times of farmyard disturbance this reduced to 48 minutes (1.25 v/h) (*ibid.*). Ratcliffe (1980) and Dory (1989) cite the increase of road traffic, walkers, campers, climbers (coastal routes are increasingly used) and second-home ownership as contributory.

Cornwall, sometimes known as 'West Barbary' (Jenkins 1970), was very much a wild outpost even as late as the C19. In 1663, 'the post' took 8 days to reach Penzance from London, and ordinary travel was much slower (>3 weeks); well into the C18, wheeled traffic was rare (*ibid.*). In the 1750s, the roads were said to be the "worst ... in all England. A great part are intolerable ... whilst most of those which have been improved are so extremely narrow and uneven that they are almost inaccessible to all kinds of wheeled vehicles... the one grand article that has so much prejudiced travellers against the county" (*ibid.*). Thereafter, upon the development of the stage-wagon (the forerunner to the stage-coach), the 'main roads' improved, but until the end of the C18, practically all merchandise was carried by mules and ponies (*ibid.*), of a breed which thrived on grass and furze (Fiennes 1698). In the mid-C18 there might, at Hayle, "usually be seen above five hundred, oftentimes a thousand animals at work [bearing coal from that port to the mines and surrounding countryside]" (Borlase 1758). At this time, "many of the country roads ... were grass-grown tracks, divided in some places by rocks or brakes of furze" (Jenkins 1970). In his original edition of *Cornwall and its people* (1945), Jenkins remarked of the old mule tracks and 'pannier-lanes' still remaining but "over-grown with brambles, furze, and other vegetation".

At the turn of C18, most inhabitants of west Cornwall were still scarcely travelled beyond their homesteads, and were "Isolated ... from the moderating influences of the outside world" (*ibid.*). In 1761, the turnpike-road still did not reach beyond Marazion "and the St Ives and Land's End districts remained, in consequence, in a splendid isolation which caused no small inconvenience to the growing mercantile interests of those areas" (G.B. Millett in loc. cit.).

It is evident from the foregoing that at the time the Chough was, by all accounts, beginning to decline seriously (the turn of the C18; see Table 3.1), the improvement in roads would be taking effect. Not only did this have a profound affect upon the mobility of the local populace, it also brought about an invasion from without. Additionally, until these times, oxen, mules, ponies and horses were the primary form of locomotive power and draught. The rough-grazing and pasture necessary to sustain this population must have been very considerable, as would the consequent organic backput into the environment. Such features of 'primitive' countryside, decreased synchronously throughout the C19 while, at the same time, the impact and repercussions of the human population increased. Corn crops and store cattle replaced dairy produce as the chief commodity off the farm (Roberson & Stamp 1941). "This change could not have come about except for the improvement of communications between Cornwall and the rest of England, especially the construction of the mainline in the [18]sixties" (*ibid.*). A similar pattern of events with local variations was probably occurring throughout the 'Celtic fringe'.

On 4 May 1859, the main railway connecting Cornwall with England over the River Tamar was opened. Balchin (1983) wrote: "subsequent events were to make this an historic date in the evolution of the Cornish landscape as thereafter the county lost its isolation and became wide open to English influences". As a result of 'the second English invasion', the economic base changed from mining and fishing to tourism, and agriculture changed from the subsistence type to more specialised dairy farming and early flowers and vegetables for export (*ibid.*). The Victorians arrived in Cornwall in large numbers, and made for the wildest stretches of coast, previously inhabited only by fishermen, tinners and crofters, and a few Choughs.

4 THE HABITAT

4.1 INTRODUCTION

As mentioned in Sections 1.3 and 3.4.6e, the Chough is believed to depend for its survival on low-intensity pastoral-based agriculture in combination with maritime cliffs. It is the most distinctive faunal link to utilise both these biomes via an imprecise transitional semi-natural zone, and it is a species which probably requires elements of all three within its yearly cycle. It seems able to exploit marginal areas, seasonal abundancies and restricted patches or foci of resources. An early precursor to the main study (Meyer 1990, see Appendix IV) proved useful in alerting me to the fact that Choughs required more than merely 'sheep-grazed pasture'. It has become apparent that the 'functional unit system' concept, as devised by Tamisier (1979) for waterfowl, and applied to Choughs by Bignal *et al.* (1989), is a useful tool in understanding the components necessary to sustain area viability for a particular species. Briefly, it takes into account the complete mix of biotopes used by all integral members of a species (not just the breeding population) within a range in order to accommodate all physical, social and behavioural needs, not merely those used at any one particular time.

While some general classification is useful, care must be exercised in the definition of the three biomes mentioned above: for example, 'cliffs' is a term often vaguely applied to any cliff region, and sometimes used to include all three, whereas, in reality, a great part will have been shaped and managed by man, *e.g.* cliffslopes grazed by sheep or introduced rabbits. Such broad categories, while useful as a starting point, especially when dealing with a species which associates with man, are, on their own, inadequate, for Choughs use elements which occur in two or more. A detailed botanical examination of precise feeding sites found a consistent selection of ecotones and edge effects which confounded National Vegetation Classification (NVC, Rodwell 1982) (4.4), which advises that samples, to be representative, need to be placed well away from boundaries. The broad habitat variables used in this study are given in Table 2.2. Selection by Choughs is affected to a certain extent by local climatic and seasonal variables (Bullock 1980).

This chapter includes three assessments of Chough habitat: present-day (4.2), past (4.5) and changes over time (4.6). It deals with Chough selection within present-day range by study area and season in Section 4.3. Each part has its own introduction, methodology and results. The botanical enquiry (4.4) is a direct consequence of observations made in connection with Section 4.3.

4.2 PRESENT-DAY BACKGROUND HABITAT ASSESSMENT

4.2.1 INTRODUCTION

The basic assessment was introduced in Chapter 2.2, where the breakdown of km^2 selected and the rationale behind their survey were described. The assessment was designed to be compatible with a similar Scottish project (Bignal *et al.* 1988).

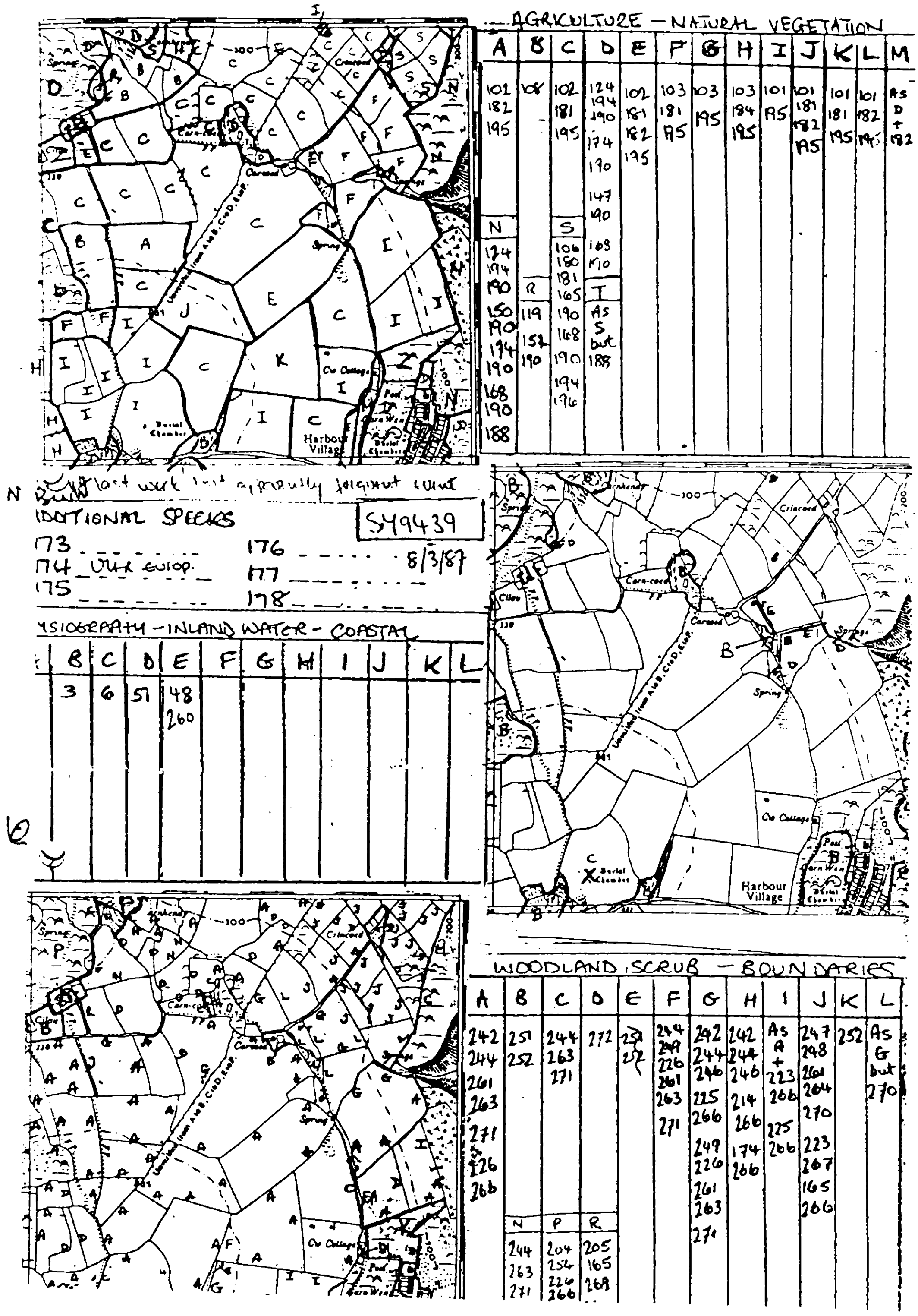
4.2.2 METHODS

The sequence of procedures was:

1. **Selection of squares.** 184 $1km^2$ arrayed on the OS grid, were selected to provide a 12% sample of land physiography and cover (see Appendix II for grid coordinates). Due to the Chough's natural habitat, coastal resolution was increased to *ca*.25% by incremental selection of additional squares (see Table 2.1 and Figures 2.2-2.5). The main aim was to describe the land-cover types (natural, semi-natural and agricultural) in a way compatible with NCC habitat mapping systems, and to enable the data to be used as a base for future monitoring of habitat change.

2. **Field mapping.** Each $1km^2$ was surveyed and mapped for features associated with agriculture and (semi-)natural vegetation as described in Section 2.2. The boundaries of distinct patches, characterised by a particular variable or set of variables, were outlined on photocopied 1:10,000 maps and labelled (see Figure 4.1a,b); the variables are after Bignal *et al.* (1988a) but more detailed NVC classification was followed for maritime cliff communities (Table 4.1).

The system was devised to be sensitive to transitional stages: *i.e.* natural vegetation partially converted to agriculture, and vegetation modified by pastoralism. This was necessary to ensure that ecological variation was described and not lost by the application of inappropriate predetermined categories.



AGRICULTURE – NATURAL VEGETATION

A	B	C	D	E	F	G	H	I	J	K	L	M
102 182 195	108	102 181 195	124 194 190 174 190 147 190 168 170	102 181 182 195	103 181 195	103 195	103 184 195	101 195	101 181 182 195	101 181 195	101 182 195	As D + 182
N	R	S	T									
174 194 190 150 190 174 190 168 190 188	119 152 190	106 180 181 165 190 168 190 194 196	As S but 188									

N Burnt last week but apparently frequent event

ADDITIONAL SPECIES

SY9439

173 ....
174 Ulex europ.
175 ....
176 .... 8/3/87
177 ....
178 ....

PHYSIOGRAPHY – INLAND WATER – COASTAL

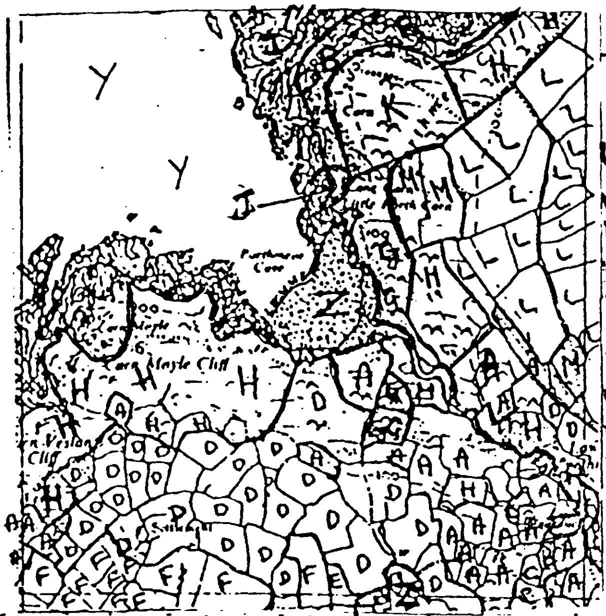
B	C	D	E	F	G	H	I	J	K	L
3	6	51	48 260							

WOODLAND SCRUB – BOUNDARIES

A	B	C	D	E	F	G	H	I	J	K	L
242 244 261 263 271 226 266	251 252	244 263 271	272	251 252	244 249 226 261 263 271	242 244 246 225 266 249 226 261 263 271	242 244 246 214 266 174 266	As A + 223 266 225 266	247 248 261 264 270 223 267 165 266	252	As G but 270
	N	P	R								
	244 263 271	204 254 226 266	205 165 169								

Figure 4.1a,b

Examples of completed $1km^2$ field survey sheet: (a) inland, (b) coastal. Numbers in columns refer to cover types, usage, features and dimensions etc (see Chapter 4.2.2)



Y
Y
K
L
M
I
H
Z
Porthmeor Cove
Carn Moyle Cliff
Little Porth Cara
D
A
F
G

A	B	C	D	E	F	G	H	I	J	K	L	M	N
109 124 194 165 198 190 180 181 182	124 194 165 198 192	118 194 152 197 R1 + C	– A – 124	102 181	186/ 187	A – 180	124 193 165 198 192	118 194 150 196	114 127	106 196 173	186 ast 181	– 103 181	

1.6/VI/87 1200 → 1300 (Rain) (3,20)
1510 → 1330

SW 4237

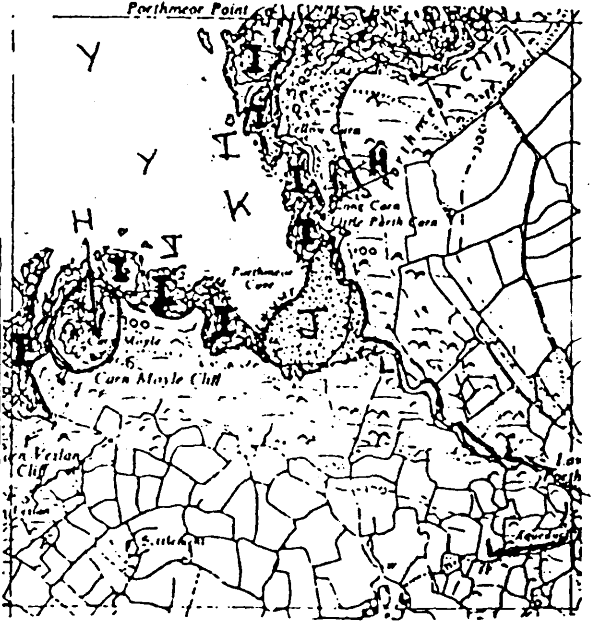
O

ADDITIONAL SPECIES

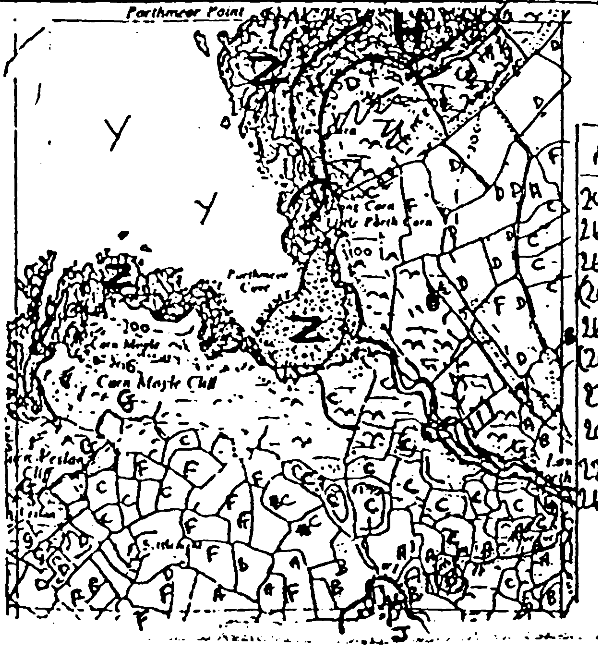
173 Plantago sp. ~~176~~ 115a – MCH (WVY)
174 ______ 177 ______
175 ______ 178 ______

PHYSIOGRAPHY – INLAND WATER – COASTAL

A	B	C	D	E	F	G	H	I	J	K	L
							3 9	27	29	26	48



Porthmeor Point
Y
Y
I
K
H
J
Porthmeor Cove
Carn Moyle Cliff
Little Porth Cara



Porthmeor Point
J
H
Y
Y
Z
Z
Porthmeor Cove
Carn Moyle Cliff
Little Porth Cara
C
F
D
G
J

WOODLAND, SCRUB – BOUNDARIES

A	B	C	D	E	F	G	H	I	J	K	L	M
242 260 263 (266) 264 (266) 271 204 226 266	270	242 266 263 204 263 270	C bat ~~270~~ 274	233 232 219 269	272	204 263 225 266	204 263 223 266 226 266	115a 126 197 191	[illegible] 251 267 252 266			

Table 4.1 Maritime influenced communities (after NVC, Rodwell 1982) used as the basis for habitat assessment (see Tables 4.2 - 4.4 for extra descriptions)

Code	Description
MC1	*Crithmum - Spergularia* maritime rock-crevice
MC4	Brassica maritime cliff-ledge
MC5	*Armeria - Cerastium* maritime therophyte
MC6	*Atriplex - Beta* sea-bird cliff
MC8	*Festuca - Armeria* maritime grassland
MC9	*Festuca - Holcus* maritime grassland
MC10	*Festuca - Plantago* maritime grassland
MC11	*Festuca - Daucus* maritime grassland
MC12	*Festuca - Hyacinthoides* maritime grassland
MG1	*Arrhenatheretum* grassland
U46	*Festuca - Agrostis* grassland
MCH	Maritime heath

3. **Analytical methods.** Completed field sheets were rasterized either by the use of automated digitising equipment or by manually transforming the discrete patches into arrays of letters by overlaying each completed field map with a 25x25 4mm^2 grid marked on a transparent acetate. Each square was scrutinised and subdivided by eye into quarters, giving 2500 20x20m subsquares of information (called pixels) per map (Figure 4.2). The integrity of the original variables was maintained and formed into appropriate combinations of pixels per row to allow analysis of the data set. Each pixel type was assigned an individual letter to correspond with the environmental patch (Figure 4.3). Various analyses were then possible using either the original arrays of unique variables or derived combinations. Letters were used in alphabetical order in the field for each map and usually had no special significance or dependence on those used in other maps. For example, 'S' on one map might denote '100% improved pasture/<5cm tall/grazed by cattle' whereas on another square, 'S' might represent 'marsh'. It was necessary, however, for onward analysis, to ascribe letters which were consistent across all squares in order to conduct patch and map-square analyses:

Figure 4.2

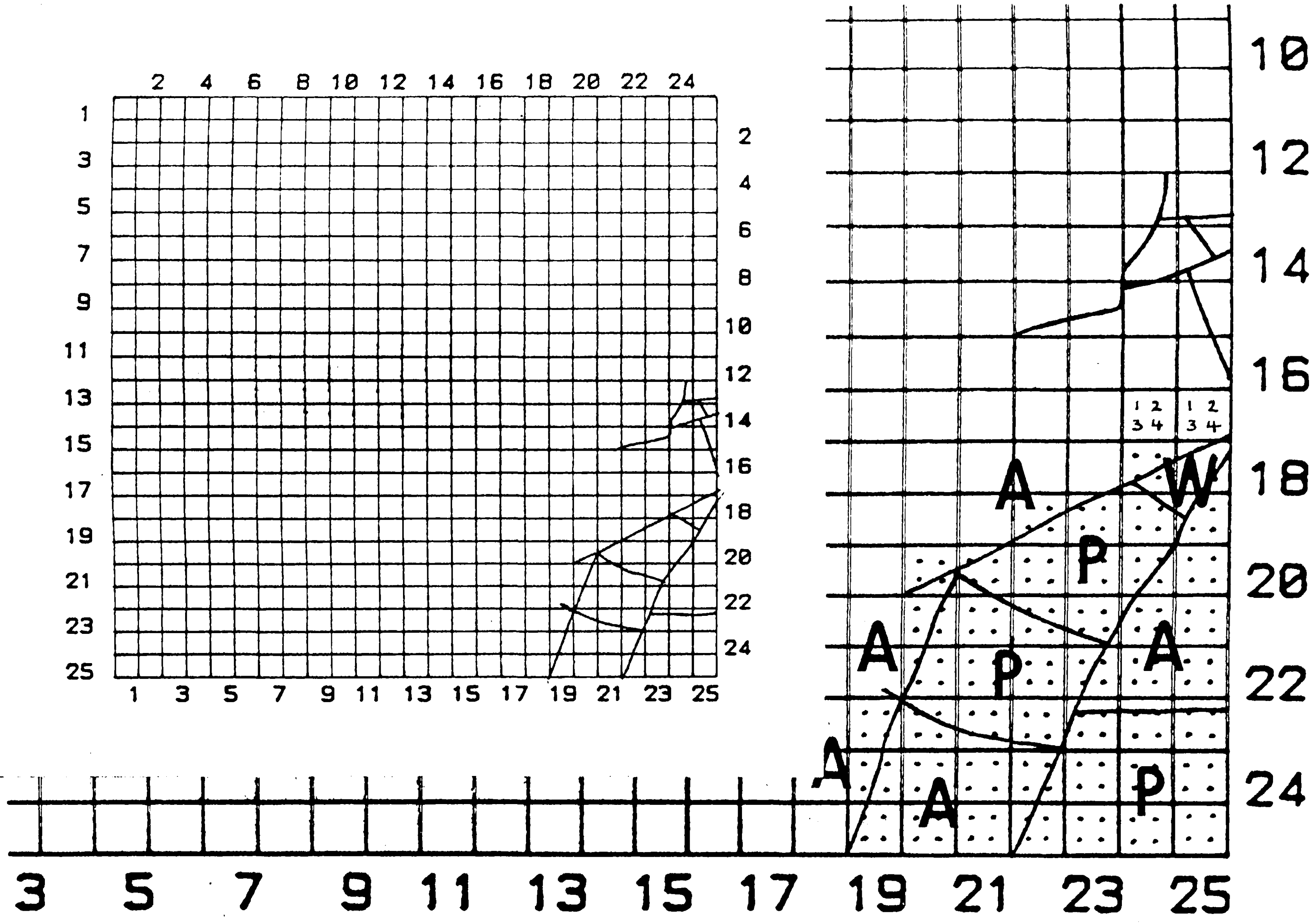
Diagram of acetate grid overlay and pixel counting rationale (row 17). Identified squares in bottom right corner would compute to:

Row 18	A*3W*4A	(A=4,W=4)	8	pixels
Row 19	A*3P*9WA*3	(A=6,P=9,W=1)	16	"
Row 20	A*5P*14A*5	(A=10,P=14)	24	"
Row 21	APAP*13A*8	(A=10,P=14)	24	"
Row 22	AP*12APA*9	(A=11,P=13)	24	"
Row 23	A*5PA*2P*2AP*17	(A=8,P=20)	28	"
Row 24	A*15P*13	(A=15,P=13)	28	"
Row 25	A*13P*15	(A=13,P=15)	28	"

* = multiplied by

Letters describe patch variable,

e.g. A = arable, P = pasture etc



2 4 6 8 10 12 14 16 18 20 22 24
1 3 5 7 9 11 13 15 17 19 21 23 25
1 3 5 7 9 11 13 15 17 19 21 23 25
2 4 6 8 10 12 14 16 18 20 22 24
10 12 14 16 18 20 22 24
3 5 7 9 11 13 15 17 19 21 23 25
1 2
3 4
1 2
3 4
A
W
P
A
P
A
A
A
P
A

Patch analysis. The field data were organised as described to produce a combination of patches which were then recoded to comply with a set consistent for all 1km^2. A 'patch' therefore equalled a set of contiguous homogeneous pixels (20x20m mapped unit) bounded by a different set or sets or the limit of the map. Data handling involved taking the environmental data from the coded fieldsheets and entering them into a computer.

Map-square analysis. This was based on the descriptions of the 1km^2 by frequencies of different pixel types. Each pixel within the square was ascribed the letter of the patch-type to which it belonged. The squares could then be described by the the quantity of pixels belonging to each patch-type (see Figure 4.3).

The data describing the observed patches were taken from each fieldsheet (see Figure 4.1). They were entered into computer as a subsidiary of the NCC land use project (Bignal *et al.* 1988a) at the Department of Biology in the Paisley College of Technology under the supervision of Professor D. Curtis and C. Moos. The TWINSPAN Cornel Ecology Program (Hill 1979) at the Institute for Terrestrial Ecology, Merlewood, Cumbria was used to classify squares and define habitat on the basis of pixel frequencies, and produce a dichotomous classification (Figures 4.4-4.6). TWINSPAN identifies indicator habitat-types and differential species, which are the attributes distinguishing the groups and governing the division at each ordinal level; all other variables are excluded.

Subsequent observational fieldwork on the Chough showed that certain factors within the natural, often steep, cliff habitat influence the usage of the semi-natural and agricultural cliff-top habitat (see Section 4.3). The prescribed criteria were deficient in three main respects: (i)

Figure 4.3

Rasterized $1km^2$ map after environmental patches have been assigned individual letter arrays.

Top, agricultural patches; bottom, boundaries: on both maps 'Y' = sea, other codes signify patch variables.

Boundaries: 'B' = boundary, 'Z' = other

S M 8839A agriculture

```
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z F F F F F F P P P P P P P P P P P P P P P P P P P P P P P M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Z Y Y F F F F F F P P P P P P P P P P P P P P P P P P P P P P P M M M M M M M
Y Y Y Y Y Y Y Y Y Y Z Y Y Y F F F F F F P P P P P P P P P P P P P P P P P P P P P P P M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y Y F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y Y F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P M M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P M M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y Y F F F F P P P P P P P P A A A P P P P P P P P P P P P P M M M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y Y F F F F P P P P P P P P A A A A A P P P P P P P P P P P M M M M M M M M M
Y Y Y Y Y Y Y Y Y Y Y Y F F F F F P P P P P P P A A A A A A P P P P P P P P P P P P P P P M M M M M
Y Y Y Y Y Y Y Y Y Y Y F F F F F F F P P P P P P A A A A A A P P P P P P P P P P P P P P P P M M M M
Y Y Y Y Y Y Y Y F F Y F F F F F F F F P P P P P A A A A A A P P P P P P P P P P P P P P P P P P P M
Y Y Y Y Y Y Y F F F F F F F F F F F F F F P P P A A A A A A P P P P P P P P P P P P P P P P P P P M
Y Y Y Y Y Y Y F F F F F F F F F F F F F F F F A A A A A A P P P P P P P P P P P P P P P P P P P P P
Y Y Y Y Y F Y F F F F F F F F F F F F F F F P P P A A A A P P P P P P P P P P P P P P P P P P P P P
Y Y Y Y F F F F F F F F F F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P P
Y Y Z Y Z Z Z F F F F F F F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P P
Y Z Y Z Z Z Z F F F F F F F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P P
Y Y Z Z Z Z Z F F F F F Z F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P P
Y Y Z Z Z Z Z F F F Z F F F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P A
Y Y Z Z Z Y Y Y Y Y F F F F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P A
Y Y Y Y Y Y Y Y Y Y F Z F F F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P P P P A
Y Y Y Y Y Y Y Y Y Y Z Z F F F F Y F F F F F F F F P P P P P P P P P P P P P P P P P P P P P P P P A
Y Y Y Y Y Y Y Y Y Y Z Z Z F F F Y Y F F F F F F F F F F A A A A P P F F P P P P A A P P H A A A A A
Y Y Y Y Y Y Y Y Y Z Z Z Y F F F Y Y F F F F F F F F F F A A A A A A F F P P P P A A A A H A A A A A
Y Y Y Y Y Y Y Y Y Y Y Y Y F F F Y Y F F F F F F F F F F F A A A A A F F P A A A A A A A A A A A A A
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z F F F F F F F F F F F A A A A F F F F A A A A A A A H A A A A A
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z F F F F F F F F F F F F F A F F F F F A A A A A A H H A A A A A
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y F F F F F F F F F F F F F F F F F F F F A A A A A A Z Z A A A A A
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y F Y Z Z F F F F F F F F F F F F F F F A A A A A Z Z A A A A A A
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Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y F F F F F F F F F F F F F Z Z Z Z Z P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z F F F F F F F F F F F F Z F Z Z P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Y Y Y Y Y Y Y Y Z F F F F F F F P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z F Z Z Z Z F P P P P P
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Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z P P P P P P P P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y P P P P P P P P P P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y P P P P P P P P P P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y P P P P P P P P P P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y P P P P P P P P P P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z P P P P P P P P P P P P P
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z P P P P P P P P P P P P
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S M 8839Boundaries

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Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z B Z Z Z Z Z Z Z B B Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Z Y Y Z Z Z Z Z Z B Z Z Z Z Z Z Z Z Z Z B B B Z Z Z Z Z Z Z Z Z B Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Z Y Y Y Z Z Z Z Z Z B Z Z Z Z Z Z Z Z Z Z Z Z Z B B B Z Z Z Z Z Z B Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z B Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B B B Z Z B Z Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z B Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z B Z Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z B B B B B Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z B Z Z Z B B Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z B Z Z Z Z Z Z B B B B B Z Z Z Z Z Z Z Z Z Z Z B B Z Z Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z B Z Z Z Z Z Z Z B B Z Z B Z Z Z Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z B B Z Z Z B B B Z Z Z Z Z B B Z Z Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z B B Z Z Z Z Z B Z Z Z Z Z B Z B B B Z Z B Z Z Z Z Z Z B B B Z Z Z
Y Y Y Y Y Y Y Y Z Z Y Z Z Z Z Z Z Z Z B Z Z Z Z B Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z Z B Z Z B B Z
Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z B Z Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z Z B Z Z Z Z B
Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z B B B Z Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z B Z Z Z Z Z Z
Y Y Y Y Y Z Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z B B B B Z B Z Z Z Z Z Z B Z Z Z Z Z Z B Z Z Z Z Z Z
Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z B B B Z Z Z Z Z B Z Z Z Z Z Z B Z Z Z Z Z Z
Y Y Z Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z B Z Z B B B B B B Z Z Z Z Z Z B Z Z Z Z Z Z
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Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z B Z Z Z Z Z Z B
Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z B Z Z Z Z Z Z B
Y Y Z Z Z Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z B Z Z Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z Z B Z Z Z Z Z Z B
Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z B B Z Z Z Z B Z Z Z Z Z Z Z B Z Z Z Z B Z Z Z Z Z Z Z B
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Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B B B Z B B Z Z B Z Z B
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z Z B B B B B B Z Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z Z Z B Z Z B Z B B B B
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Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z B Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z B Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z B Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z B Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z B B B
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z Z B Z Z
Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z B Z Z Z
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Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Y Z Z Z Z Z Z Z Z Z Z B Z Z B
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a minimum mappable unit of $20m^2$ was not sufficiently sensitive to detect the smaller patches of complex mosaics used by Choughs within these natural habitats (see Section 4.4); (ii) the contour effect which, without correction, under-represents cover scores as assessed from 2-dimensional maps, *i.e.* the steeper the gradient, the closer together the contour lines, and the poorer the map resolution, until on a vertical cliff, map resolution is zero - a serious problem with a cliff-living species; and (iii) the intensive nature of the habitat survey prevented more than anecdotal recording of Chough usage within the sample during the study period. These problems were redressed in the assessment of habitat within the observational study areas (see Section 4.3.3b, Table 4.11). There is an opportunity for follow-up work specifically designed to relate the results of the original habitat survey to Chough usage.

4.2.3 RESULTS

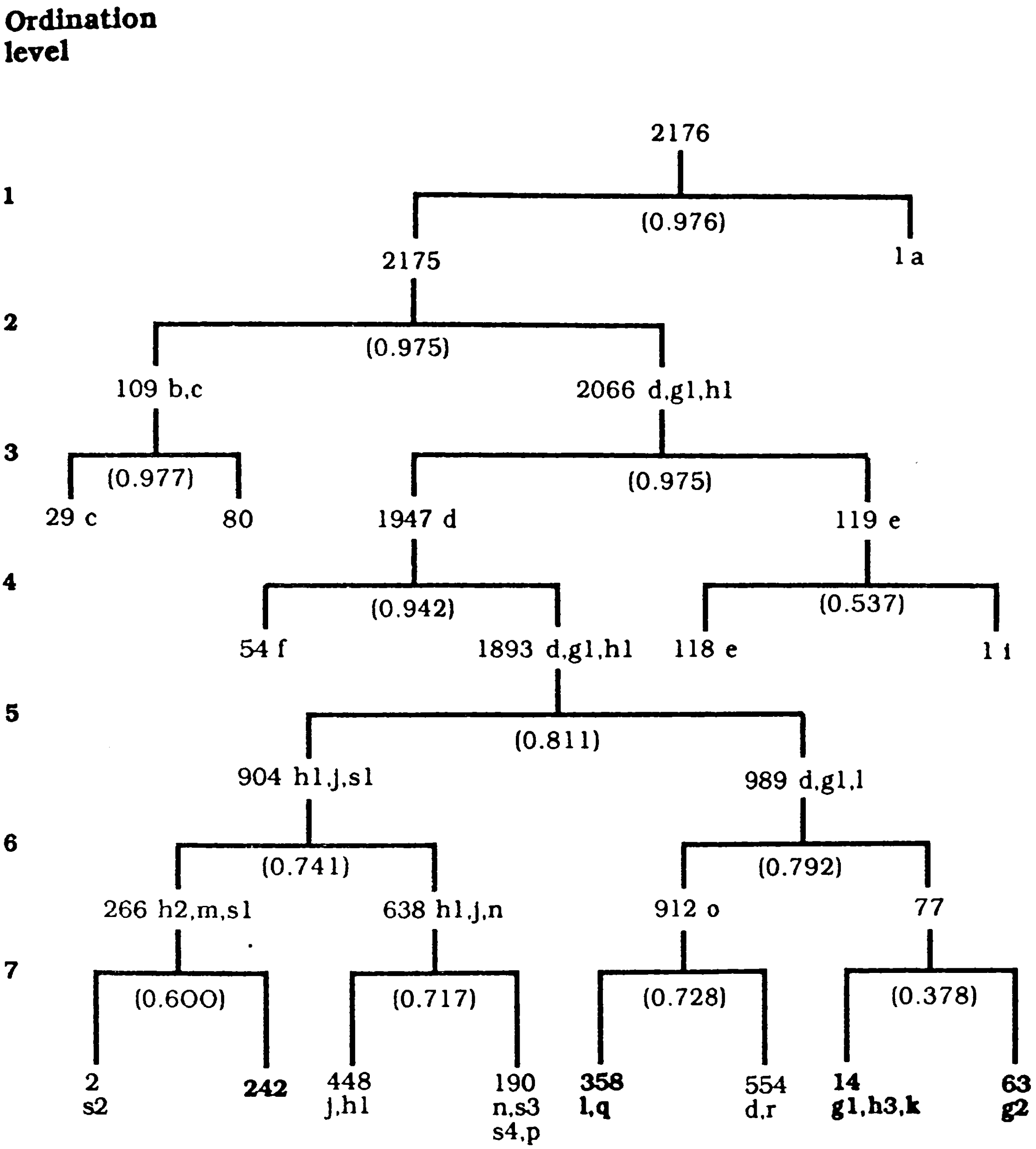
The original TWINSPAN classification of all mapped patches (n=2176) is shown in Figure 4.4. As an example and for illustrative purposes, no selections or weighting were applied at this stage and yet the results show a good dichotomy between typical modern agriculture and habitats with attributes which are considered, on the basis of the literature and subsequent fieldwork, to be advantageous to Choughs. At level 6, 989 patches are selected, identified by the positive (for Choughs) attributes 'old-/improved pasture - cattle-grazed'. At the next level, on the left side, 266 patches are selected with the positive attributes of *Festuca* maritime grassland; however, the height profile (10-30cm) suggests disadvantageous under-grazing. At the final level (8), four end-groups of varying degrees of potency for Choughs are indicated; these are differen-

Figure 4.4

Hierarchical TWINSPAN habitat classification, Wales and Cornwall. Emboldened end groups contain possible attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level: greater value (0.001 – 1.0) + greater sample size (n = patches) = better dichotomy

Key (bold indicates possible Chough attributes included in end groups):

a	reclaimed land	**h2**	**vegetation <30cm tall**
b	root crop	**h3**	**vegetation <10cm tall**
c	other crop	**i**	**burnt**
d	improved pasture	j	*Pteridium* (bracken)
e	cereal	**k**	**Old/permanent pasture**
f	ploughed	**l**	**Old improved pasture**
g1	**cattle-grazed**	**m**	**MC8 (see Table 4.1)**
g2	**sheep-grazed**	n	marsh
h1	vegetation <1m tall	o	reseeded ley
p	flush		
q	**hay**		
r	silage		
s1	***Festuca* spp.**		
s2	*Ammophila arenaria*		
s3	*Juncus* spp.		
s4	*Iris pseudocorus*		


Ordination level
1
2
3
4
5
6
7
2176
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2175
1 a
(0.975)
109 b,c
2066 d,g1,h1
(0.977)
29 c
80
(0.975)
1947 d
119 e
(0.942)
54 f
1893 d,g1,h1
(0.537)
118 e
1 i
(0.811)
904 h1,j,s1
989 d,g1,l
(0.741)
266 h2,m,s1
638 h1,j,n
(0.792)
912 o
77
(0.600)
2
s2
242
(0.717)
448
j,h1
190
n,s3
s4,p
(0.728)
358
l,q
554
d,r
(0.378)
14
g1,h3,k
63
g2

tiated by, on the right side: (i) 'old-improved pasture - hay' (358); (ii) 'sheep-grazing' (63); and (iii) 'cattle-grazed - low profile - permanent pasture' (14); whereas on the left side, 2 patches, indicated by *Ammophila arenaria* (Marram grass), are selected out, leaving the under-grazed maritime grassland as a potentially favourable habitat. Therefore 435 patch-types with positive attributes are selected, with a further 264 of high potential.

The same treatment was applied to the Welsh and Cornish data independently; the results are shown in Figures 4.5a-b. By these means, 742 patches are indicated which carry good Chough attributes, 507 in Wales and 235 in Cornwall. In Wales (Figure 4.5a), an additional 48 have quite high potentiality as indicated by the inclusion of sheep-grazing and old-improved pasture but this group also contains the indicators 'improved - reseeded pasture' which seem less advantageous, at least in southern Britain (4.3). The '110' group is primarily maritime grass with heathland components but of a high vegetation profile and will contain many of the patches in the 266 mentioned above. The primary group in Wales is the '397' group, best summarised as low profile (<10cm) variably aged grassland, grazed by all the commoner domestic stock: cattle, sheep and horses.

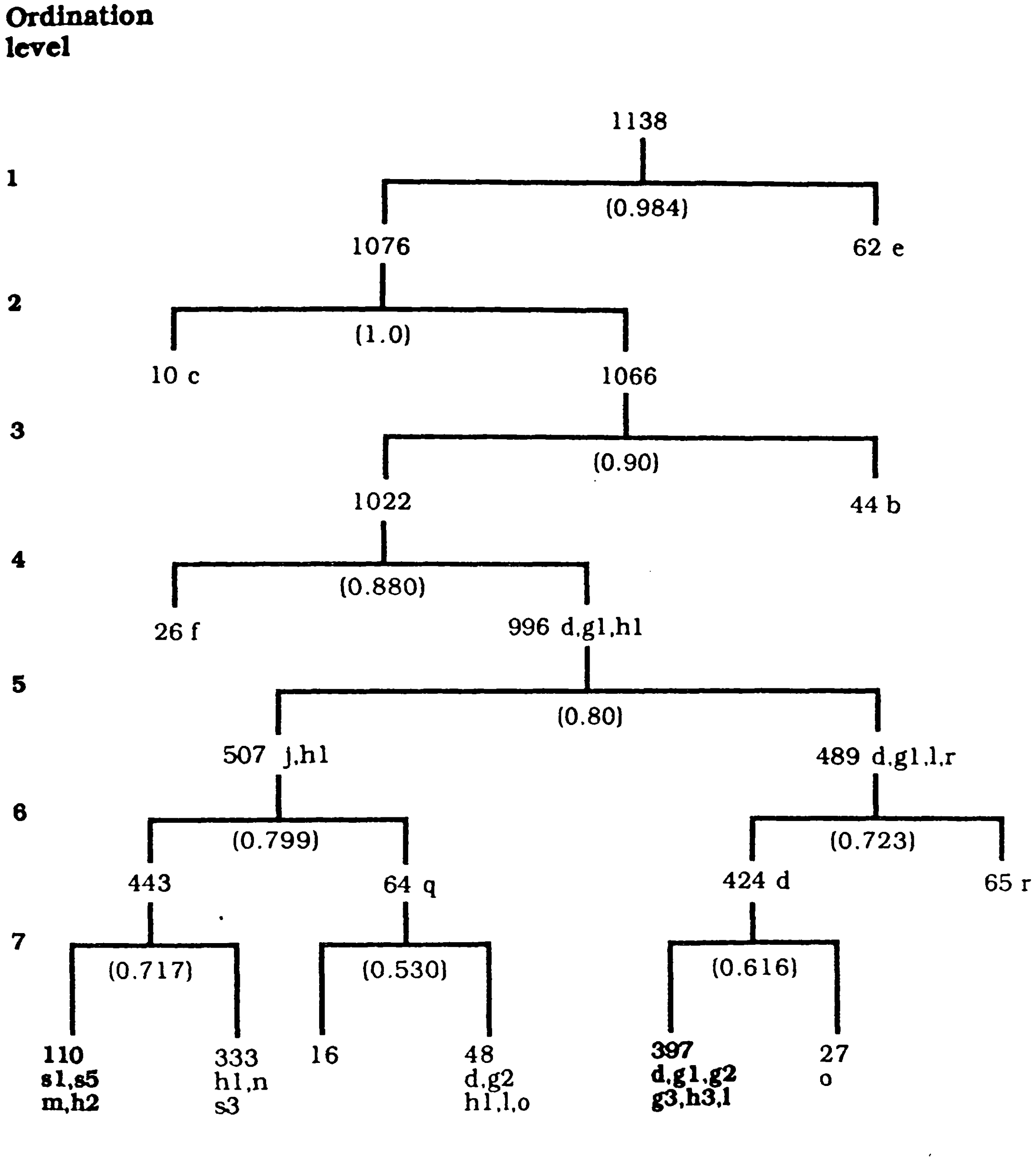
The Cornish data analysis (Figure 4.5b) does not reveal short or even medium-short vegetation as differentially important. The largest group numerically is the '364' group indicated by tall bracken, indicative of 35.1% of all mapped patches. The equivalent group within the Welsh matrix is the '333' group which, as can be seen at level 6, contains the patches differentiated by tall bracken (this represents 29.3% of all patches). The primary end groups in Cornwall, identified by TWINSPAN, and dichotomised by a high eigenvalue (>0.700), are the '162' group and,

Figure 4.5a

Hierarchical TWINSPAN habitat classification, Wales only. Emboldened end groups contain advantageous attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level

Key (bold indicates favourable Chough attributes included in end groups):

b	root crop
c	other crop
d	improved pasture
e	cereal
f	ploughed
g1	**cattle-grazed**
g2	**sheep-grazed**
g3	**horse-grazed**
h1	vegetation <1m tall
h2	**vegetation <30cm tall**
h3	**vegetation <10cm tall**
j	*Pteridium* stands
l	**Old improved pasture**
m	**MC8 (see Table 4.1)**
n	marsh
o	reseeded ley
q	hay
r	silage
s1	***Festuca***
s3	*Juncus*
s5	***Calluna vulgaris***


Ordination level
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3
4
5
6
7
1138
(0.984)
1076
62 e
(1.0)
10 c
1066
(0.90)
1022
44 b
(0.880)
26 f
996 d,g1,h1
(0.80)
507 j,h1
489 d,g1,l,r
(0.799)
443
64 q
(0.723)
424 d
65 r
(0.717)
110
s1,s5
m,h2
333
h1,n
s3
(0.530)
16
48
d,g2
h1,l,o
(0.616)
397
d,g1,g2
g3,h3,l
27
o

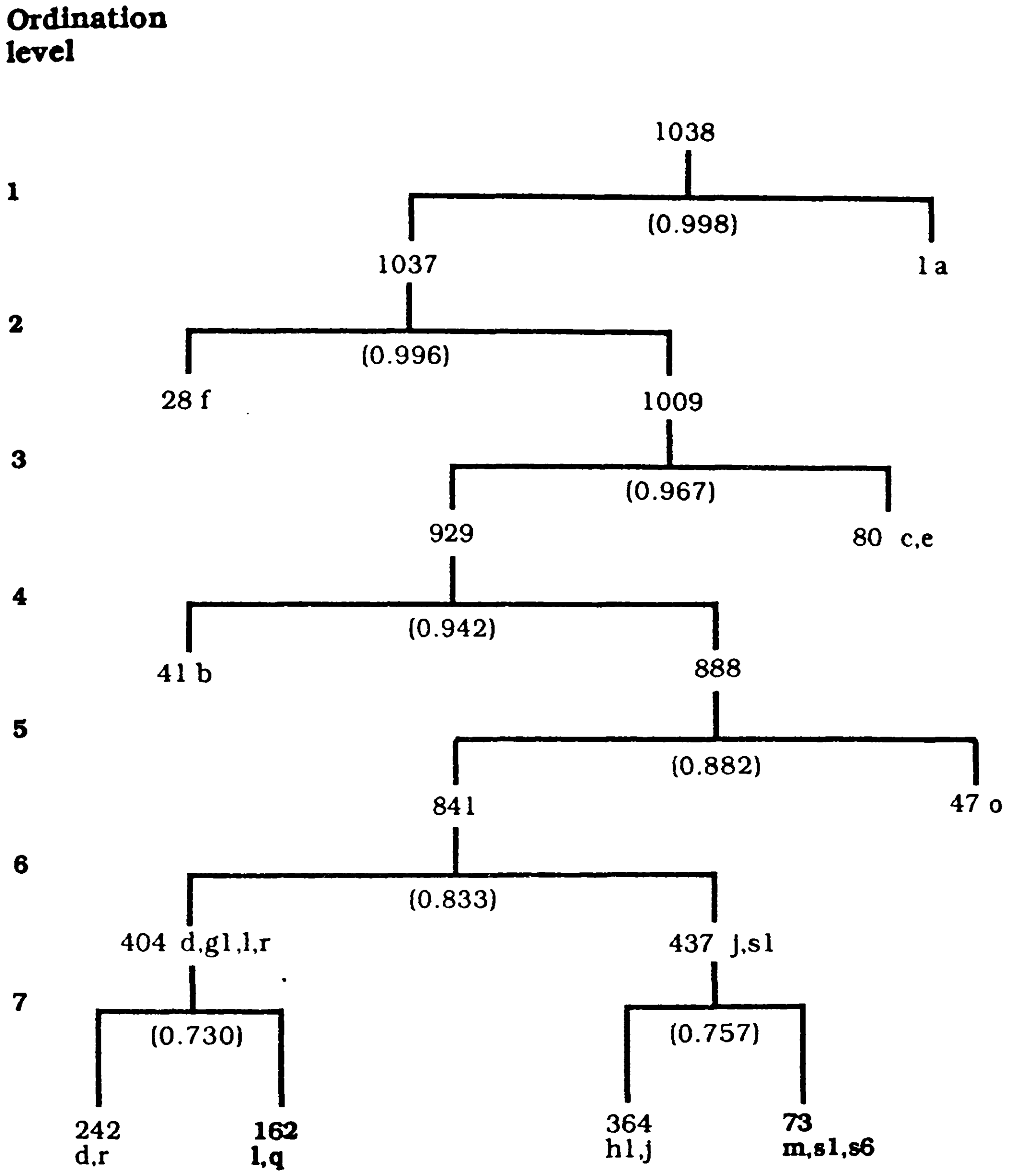
Figure 4.5b

Hierarchical TWINSPAN habitat classification, Cornwall only. Emboldened end groups contain advantageous attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level

Key (bold indicates favourable Chough attributes included in end groups):

a	reclaimed land	**gl**	**cattle-grazed**
b	root crop	hl	vegetation <1m tall
c	other crop	j	*Pteridium* stands
d	improved pasture	**l**	**Old improved pasture**
e	cereal	**m**	**MC8 (see Table 4.1)**
f	ploughed	o	reseeded ley

q	hay
r	silage
s1	***Festuca***
s6	***Armeria maritima***


Ordination level
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2
3
4
5
6
7
1038
(0.998)
1037
1 a
(0.996)
28 f
1009
(0.967)
929
80 c,e
(0.942)
41 b
888
(0.882)
841
47 o
(0.833)
404 d,g1,l,r
437 j,s1
(0.730)
(0.757)
242 d,r
162 l,q
364 h1,j
73 m,s1,s6

especially, the '73' group, which is exclusively maritime. The '242' group indicates intensive farming, and yet in Wales these elements are found the '489' group at level 6 which also contains the Chough-positive '397' end group, suggesting that the mix of habitats in Wales is more varied.

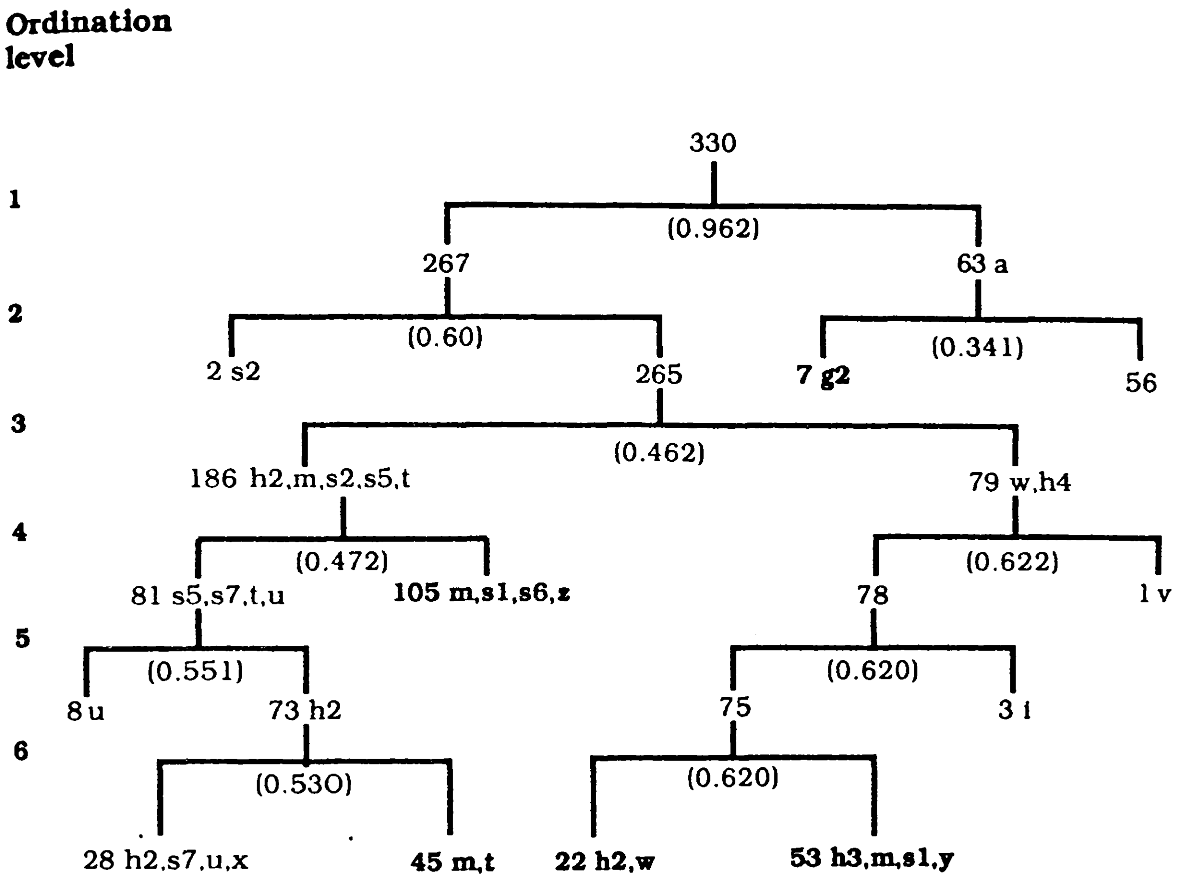
It is important to remember that the data presented here are from the entire region, and therefore contain data from a high proportion of inland $1km^2$ (see Figures 2.2 - 2.5), well outside current Chough range. It was decided not to attempt a classification based on a somewhat arbitrary selection of coastal squares but to create a dichotomy based essentially on the natural and semi-natural attributes indicated in Figure 4.4 since these already contain typical coastal characteristics. The result is shown in Figure 4.6; the emboldened end groups are those which have a high Chough value. The lower eigenvalues are well within validity limits (C. Moos pers. comm.). One hundred and thirty two patches (40%) are differentiated by a vegetation profile of <10cm; the balance is, not unexpectedly, comprised mainly of scrub, heath and longer grassland of variable but generally longer height.

Figure 4.6

Hierarchical TWINSPAN classification of natural and semi-natural habitat types, Wales and Cornwall. Emboldened end groups contain advantageous attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level

Key (bold indicates favourable Chough attributes included in end groups):

a	reclaimed land
g2	**sheep-grazed**
h2	**vegetation <30cm tall**
h3	**vegetation <10cm tall**
h4	**vegetation <5cm tall**
i	**burnt**
m	**MC8 (see Table 4.1)**
v	aquatic macrophytes
w	**species-rich grass**
x	moor grass
y	**rough grazing**
z	**therophytes**
s1	***Festuca***
s2	*Ammophila arenaria*
s5	*Calluna vulgaris*
s6	***Armeria maritima***
s7	*Erica cinerea*
t	**MCH (see Table 4.1)**
u	maritime scrub


Ordination level
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2
3
4
5
6
330
(0.962)
267
63 a
(0.60)
2 s2
265
(0.341)
7 g2
56
(0.462)
186 h2,m,s2,s5,t
79 w,h4
(0.472)
81 s5,s7,t,u
105 m,s1,s6,z
(0.622)
78
1 v
(0.551)
8 u
73 h2
(0.620)
75
3 i
(0.530)
28 h2,s7,u,x
45 m,t
(0.620)
22 h2,w
53 h3,m,s1,y

4.3 SELECTION OF HABITAT BY CHOUGHS

4.3.1 INTRODUCTION

When members of a species select one habitat to exploit in preference to another nearby, an understanding of the factors which effected the selection is instructive about the particular species' ecological requirements. Appropriate habitat selection processes are likely to reduce the effects of competition. Within sympatric congeners, the degree of adaptive radiation of bill morphology, for example, is known to be sensitive to low abundancy food supplies (Schoener 1965). It is also possible to gain an insight into a particular species' niche by examples of convergency; for example, the decurved beak of the Curlew, not unlike the Chough's, has been shown to facilitate the shallow probing of subterranean invertebrate passages (Davidson *et al.* 1986; see Section 1.3.1). The tit family (Paridae) has provided much of the evidence for selective habitat use in birds (*e.g.* Kluijver 1951, Kluijver & Tinbergen 1953, Gibb 1954, Lack 1966, Royama 1970, Krebs 1971, van Balen 1973, and Krebs *et al.* 1977). For example, tits in the Old World, and chickadees in the New World, which exploit coniferous woodland in preference to deciduous woodland, tend to have finer and more sharply pointed bills with which to gather the particular invertebrate prey found at the base of conifer needles (Lack 1971).

As with the Curlew, the Chough is specialised in the mandibulation of invertebrate prey in subterranean passages and generally probes and 'investigates' for food. 'Good' Chough habitat might be summarised as 'invertebrate-friendly' and 'invertebrate-accessible': these are usually natural or semi-natural systems. However, of course, not all natural habitats within their current range are utilised by Choughs: if maritime scrub succeeds the abandonment of grazed clifflands, it would be the previous state that benefited Choughs (*i.e.* pastoralism), the natural succession representing a deterioration in the suitability of habitat for Choughs. It was necessary, therefore, in this study, to relate assessment criteria directly to known Chough usage. This was achieved by including on the benefit, or plus, side of the equation any habitat which Choughs use regularly and on the negative side any which they do not. The resulting categorisation could then be examined to see where a particular human activity lay, vis-a-vis benefit to Choughs; *i.e.* on which side of the equation did it fall. Maritime scrub may be regarded as man-influenced secondary habitat or non-Chough-friendly natural habitat but it is equally negative. Grassland morphology depends on extrinsic, climatic and biotic factors, and usage by man, such as his stocking, mowing and ploughing regimes, the application of chemicals etc. (Moore 1966), and just by his sheer physical presence (Liddle 1975). A history of rough grazing or low-input cultivation or pastoralism would be indicated by 'permanent', 'old-', 'semi-' or 'un-improved' grassland, *i.e.* beneficial influence by man. There are likely to be 'grey areas' at the threshold from low- to high-intensity agriculture, where Chough usage changes or falls off. Also, it must be remembered that all areas accessible to man are vulnerable to reversion or drastic change. Such change, *e.g.* ploughing, is usually damaging but not inevitably so: scrub cleared perhaps by burning, can suddenly release habitat for Chough exploitation (Haycock & Bullock 1982); Owen (1985) recorded that all heathland feeding incidents in one year of his study in Ceredigion (north of study area W1) were in a single mown area (n=34hr). Similarly, rotation from arable to improved grass could provide a valuable winter dung resource. Only inaccessible islets and the steeper cliffs are generally beyond man's direct long-term influence.

Animals influence each other in selection of localised food resources, and they may remain in a known area rather than increase energy expenditure by searching for alternative sites (Norberg 1977). Optimal foraging has been most studied with intraspecific groups or solitary predators (see, *e.g.* Perrins & Birkhead 1983). Cost of feeding is altered by the spatial distribution of prey and its visibility, but it is usually implicitly assumed that flock-size of predators (even if n=1) is near optimal. If so, various benefits must accrue to the co-operating individuals of flock-species that are lacking when the flock is at sub-optimal size. Ward & Zahavi (1973) advanced the theory that communal roosts act as 'information-centres' for food-finding, and Still (1989) discussed the hypothesis in relation to Choughs on Islay, where the species is not declining, and is considered to be at least stable or probably expanding at an historically high level (Easterbee & Bignal 1989). She concluded that it was important for Choughs to roost in high numbers near good feeding areas.

It is not known whether the Chough population in West Wales is stable; an apparent low-level stability (Bullock *et al.* 1985) could be disguising an ageing population or one bolstered by recruitment from elsewhere (*e.g.* Bardsey). The survival of breeding birds will exceed that of the population as a whole if opportunity to breed is related to social status and competitive ability (Perrins 1971); non-breeding birds might be forced to live in sub-optimum habitats. Whether stable or not, density and range is at a level well below that seen on Islay; observed flock size never exceeded 20 in the study-range of 950ha, compared to a maximum of 120 on Islay (*ca*.30,000 ha of Chough range, after Bignal *et al.* 1988). Occasional larger flocks (>30) are seen however (J. Donovan pers. comm.). There were no large communal roosts to serve as information-centres in my

Dyfed study areas; all roosting appeared to be in small familial groups, but birds were not marked. If Dyfed is currently at carrying capacity, then a measure of actual Chough usage is perhaps of more value than a hypothetical comparison against idealised optimum conditions. For these reasons, the habitat usage data is presented in both aggregated (over all time) and disaggregated format (mean time per day) for different habitats and study areas (4.3.2). In Section 4.3.3b, usage in the study areas is measured against availability and by season; and the habitats for this purpose, unlike in Section 4.2, are described exclusively with the Chough in mind.

4.3.2 METHODS

It has been stated (4.1) that Choughs exploit marginal resources; they are characteristically able to find and exploit small pockets of suitable habitat within broader tracts of less favoured terrain. I was interested in a finer definition of habitat (its component structure) than that employed by Bullock (1980), Roberts (1983) and Owen (1985), but it was not possible to assess accurately the available area of each habitat component because of the scattered, overlapping, temporally variable and often minimal extent of some, *e.g.* exposed substrate (4.3.4). It is, though, possible to state, for example, that some (semi-)natural habitats have exposed substrate as a constant feature (*i.e.* therophyte communities - winter sensitive annuals). So, of course, do drilled and reseeded leys but these are transitory features of an intensive (non-invertebrate friendly) agriculture, and are not, therefore, (semi-) natural.

Time spent foraging in different habitats was used to measure habitat selection (4.3.3). While aggregated time across all observation periods was empirically valuable in demonstrating the kinds of habitats most utilised by the Choughs under observation, a potential statistical problem was engendered by the lack of independence between individuals within groups of feeding Choughs, and between the individual time units, *i.e.* minutes. This was overcome to some extent by calculating the mean proportion of time per group per pursuit period spent in each habitat type, thereby taking each observational period as an independent sample. Aggregated time was used as a means of identifying and assessing components, which could then be subjected to more rigorous analyses.

The main biomes used by Choughs formed the fieldwork base for land-type classification. They were:

1. **Maritime cliffs: natural.** Inaccessible to casual visitation by man and his livestock; includes areas dominated by rock, islets and steep slopes; often subject to severe exposure and salt deposition (Malloch 1972) which gives rise to unique botanical communities characterised by erosion zones and sparse open communities of therophytes (Rodwell 1982).

2. **Agricultural: man-made.** The largest and most homogeneous category. Land usually enclosed and under permanent but not necessarily rotational management. Arable land is mainly cereal crops, occasionally roots and brassicas. Buildings and other artefacts did not occur significantly in the study areas (1.35% of study range, see Table 4.11).

3. **Transitional: man-influenced or semi-natural.** Difficult to demarcate since farmland often blends into cliffland through a series of ecotones. These may be used by man at a low-level or only intermittently. Man influences habitats indirectly as well: one example is rabbit-grazed maritime grassland (rabbits are not indigenous British fauna but are now naturalized). Is such a habitat man-influenced? In order to arrive at a sensible and valid set of criteria, applicable to all likely

Table 4.2 Categories of maritime and sub-maritime grassland communities after NVC (National Vegetation Classification). A suite of closed swards with Red fescue *Festuca rubra* generally abundant, and understood in terms of species balance (see also Table 4.3)

Category	Description
MC5 *A. maritima* *Cerastium diffusum* maritime therophyte community	Constant spp. *F. rubra*, *Plantago coronatus*, *Sedum* sp. Characteristic of excessively-draining, often very shallow soils at all levels on rocky, where skeletal mixtures of mineral/organic matter acumulate, or near rock outcrops where deeper soils thin out. Generally out of reach of stock and ungrazed, even where there is no cliff-top enclosure.
MC8 *Festuca rubra* - *Armeria maritima* maritime grassland	A generally closed sward, dominated by *F. rubra*, which often forms a thick mattress. *A. maritima* often abundant as scattered bulky cushions. The most maritime of the grasslands. Generally occurs on steep to moderate slopes up to *ca*. 50m a.s.l., but can also occur on level areas, *i.e*. Gateholm Island (Marloes study area); receives a lot of salt-spray.
MC9 *Festuca rubra* - *Holcus lanatus* maritime grassland	Extra constant spp. *Plantago lanceolatus*, *A. maritima*. Closed fairly low-growing but often rather rank/tussocky. Usually dominated by *F. rubra*
MC10 *Festuca rubra* - *Plantago* spp. sub-maritime grassland syn. 'Plantago sward'	Constant sp. *Agrostis stolonifera*. Closed very short and distinctive tight clifftop sward, generally dominated by *F. rubra* and *Plantago* spp., especially *P. maritima*, some *A. stolonifera*. A grazed equivalent of MC9 and possibly also MC8
MC11 *Festuca rubra* - *Daucus carota* sub-maritime grasland community	Constant sp. *Dactylis glomerata*. A fairly short and rather tussocky sward, of which *F. rubra* is the dominant grass. Most common on chalk and limestone cliffs of south coast W to Dorset and S Wales; isolated occurrences in SW England
MC12 *F. rubra* - *Hyacinthoides non-scripta* maritime bluebell community	Para-maritime: constant sp. *Holcus lanatus*. scattered *Rumex acetosa* and ocasionally *Daucus carota*. Occurs at same level as maritime heath grading from MC9 below.
MG1 *Arrhenatheretum elatioris* grassland	Sometimes encountered on maritime cliffs where well-drained soils occur with slight maritime influence, often grades seaward into MC9
U46 *Festuca* - *Agrostis* grassland	Short tight sward dominated by *F. ovina* & *F. rubra* and *Agrostis capillaris*, often encountered on clifftops with neutral to acid grassland. Might be derived from maritime heath by heavy grazing

Table 4.3 Categories of maritime rock crevice and cliff ledge communities (after NVC) observed to support Chough feeding events

Category	Description
MC1 *Crithmum maritmum* - *Spergularia rupicola*	The typical rock crevice sub-community normally lacks *Inula crithmoides*.
MC2 *Armeria maritima* - *Lingusticum scoticum*	Constant sp. *Festuca rubra*. Low growing, very open, rooted in rock crevices, strongly influenced by substrate. No species truly dominant. Not in Wales or Cornwall.
MC4 *Brassica oleracea*	Cliff ledge community. The *Beta vulgaris* ssp. *maritima* sub-community includes this type plus *F. rubra*, *Dactylis glomerata*, *Daucus carota* ssp. *gummifer* and *Brassica oleracea*

Table 4.4 Agricultural grasslands

Category	Description
RS Reseed (ley)	Grass sown in current or previous year
IP Improved pasture	< 5 years old. Short term grassland or ley, shown by evidence of ploughing, bare soil between grass plants (dominated by single sp.), scarcity of broad-leaved species (< 5-10/sq. m)
S-IP Old- or semi-improved pasture	Older IP - longer term grassland usually in enclosed land with a higher density of grass and herb species (*ca.* > 10sp/sq. m)
OP Old or permanent pasture	Unimproved pasture, no evidence of ploughing, generally species- and herb-rich

eventualities, it was decided to begin by differentiating at a point between man-made intensive agricultural land, which is known to be little used by Choughs, and semi-natural land subject to lower levels of manipulation, *e.g.* permanent pasture, trampled natural vegetation etc. (man-influenced). For the main purposes of this study, therefore, (1) and (3) are combined into 'cliffs/non-intensive agriculture'. Grassland can be complex and is found in (1), (2) and (3) (see Tables 4.2 & 4.3). The main differentiating criterion for this study was permanency (*i.e.* >5-7 years was regarded as 'permanent pasture') and absence of top-dressing (*i.e.* biocides and fertilsers).

Since Chough activity concentrates very largely on foraging, accounting for well over 90% of active time (see Chapter 6), a detailed refinement of these broad classes was necessary in order to establish as precisely as possible exact habitat requirements. Of the 24 major categories or components selected (see Table 2.2), 21 are not dependent on intensive farming methods. Of the remainder, a further 3/8 of the specified types are not necessarily so; only categories 15 and 22a-c are usually the result of a more intensive agriculture.

All observed feeding sites were inspected, where accessible, after the birds' departure (or examined with a telescope if not accessible) for their patch physiography and vegetation characteristics. During pursuit periods (2.5.2), they were marked for later attention. Usually it was possible to ascertain the precise location of a feeding point by the presence of field signs (probe holes, disturbed ground, faeces, etc.). Field notes recorded such physiographical detail as botanical communities, and grazing regime where present.

An assessment of usage lumped over time 'FCMs' (Feeding Chough Minutes) was obtained by multiplying FC by M, where FC is the number of feeding Choughs, and M, the minutes spent feeding. This method was used to gain a broad overview of Chough habitat selection since it could include all incidental feeding observations, together with those recorded by volunteers. Mean proportion of feeding time (PFT) spent by individuals observed in different habitats during dedicated pursuit days was used as the basis for more rigorous statistical analyses which allocated each feeding event into an exclusive category (4.3.3). FCMs were related to availability by dividing by the amount of habitat available. Owen (1985) employed the equivalent of FCMs in his study at Lochtyn, to the north of Mwnt in Ceredigion, but used only 6 habitat variables (*rock dominant*, *short grass*, *long grass*, *thrift*, *sheep bare* and *heath*).

Feeding sites may be described in a variety of ways, the value of any being determined by the inquiry in hand. For example, one bout, selected at random, took place on a (i) *cliff* (ii) *-top* (iii) *path* comprised of (iv) *short* (v) *herb-rich* (vi) *maritime-grass* which had been (vii) *sheep-grazed*, shown by the evidence of (viii) *old dung*. It is the combination of two or more of these 8 features that provide the attraction to Choughs. This form of presentation, though, provides a way of assessing the selection by Choughs of particular components or broader habitats but care should be exercised in their inter-relation, and for this reason they are not ranked. To overcome the problem of inter-relation, componental use was arranged hierarchically in order to establish the location of each within a broader context.

To relate usage or selection to availability (4.3.4), it was necessary to use habitat categories which were sufficiently broad to (i) be measured reasonably accurately and consistently, and (ii) form an identifiable standard of use outwith the study range. It would also be valuable to be able to relate this study to the results from other Chough autecological studies (*e.g.* Bullock 1980, Warnes 1982, Roberts 1985). For these reasons, dung and the component elements described in Section 4.3.3 were excluded. All feeding observations were allocated a biome category (dung events were placed in the host pasture habitat). Areas of biotopes in the study areas were calculated with a Cherry digitizer bit-pad.

4.3.3 RESULTS

4.3.3a FEEDING TIME SPENT IN DIFFERENT HABITATS

An indication of the relative importance of different components which build the habitat structure is given in Table 4.5. It is important to remember, regarding these data, that the components are not necessarily mutually exclusive but this array provides a convenient means of showing variability in the usage of different habitat components. The variability is at least partly explained by variation in availability across the study areas (4.3.3b). If West Wales is regarded as a study region, of which the study areas form a representative sample, the combined (=regional) percentage provides a representative view of West Wales as a whole, against which habitat selection in the individual study areas can be compared.

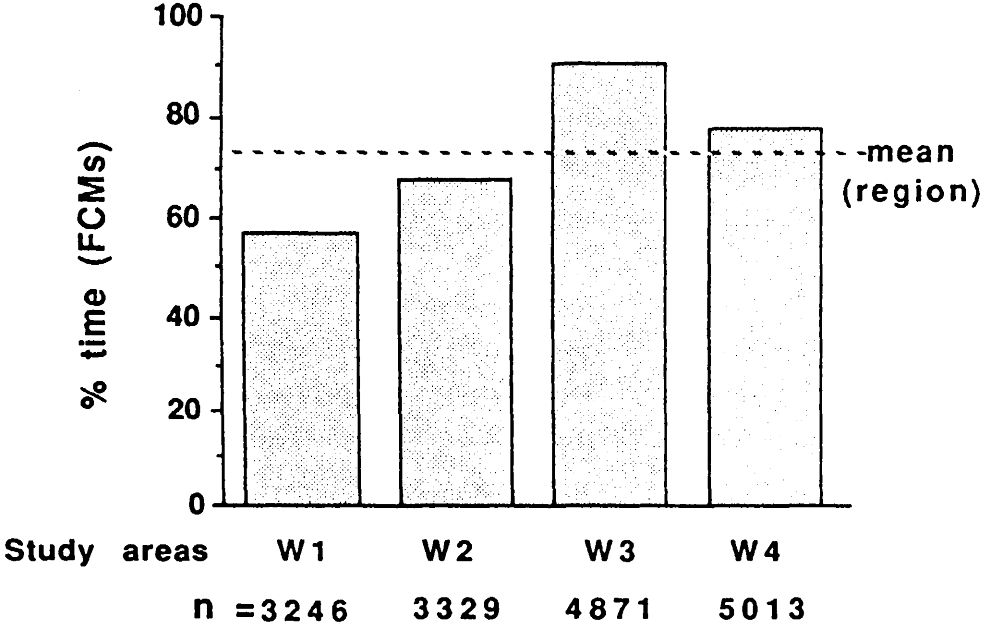
The cliff complex is the main biome, accounting for a mean feeding time of nearly 75% (Figure 4.7). Cliff-slopes with open and/or short vegetation caused by exposure and/or grazing pressure occupied at least 35% of FCMs. When grazed by domestic livestock, they form part of the semi-

Table 4.5 Habitat components observed to be selected by Choughs in all Welsh study areas. Components are not mutually exclusive and may occur in more than one category. Category no's refer to Table 2.2. Study areas: W1 = Mwnt-Cemaes, W2 = Strumble, W3 = Newgale-Solva, W4 = Marloes

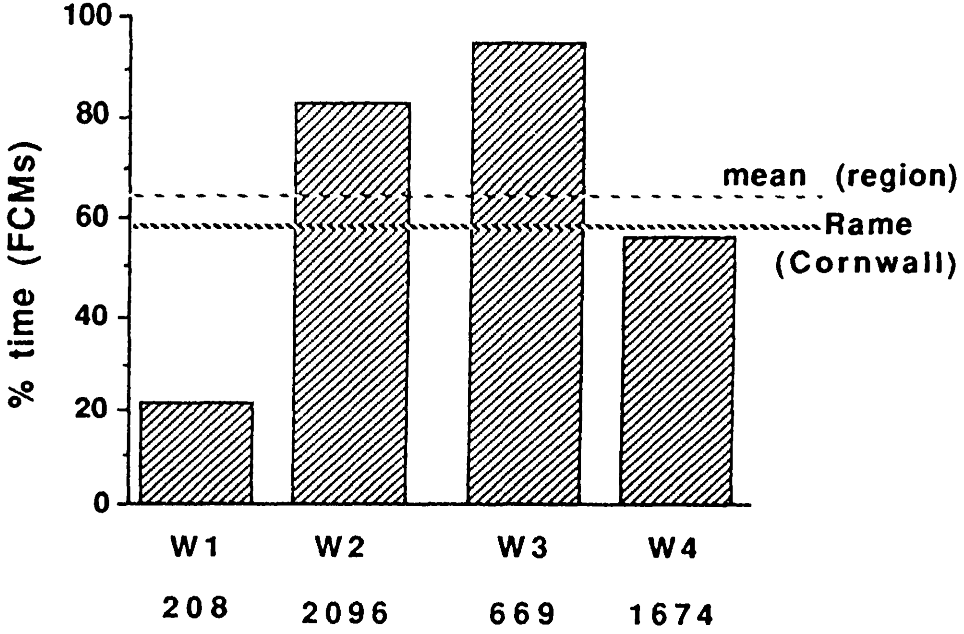
CATEGORY		%PCMs IN STUDY AREAS				
		W1	W2	W3	W4	Combined/ Regional
1	Cliffs (1a-e + 2 + unspecified)	57.1	50.5	58.2	71.3	64.5
	[Cliff complex (1 + semi-natural)	57.8	68.4	92.9	78.0	74.3]
5	Exposed substrate	21.5	20.2	57.4	58.9	40.5
1c	Cliff-slope	24.4	30.9	50.95	35.1	35.2
3	Rock-vegetation/earth interface	19.7	31.5	32.4	29.1	28.0
6	Maritime grassland	12.4	15.4	55.3	14.3	23.8
11	Ant-created habitat: hills etc.	12.0	4.9	46.9	21.5	21.4
1e	Cliff-crevice (> 50% rock)	7.4	3.9	9.9	24.1	21.1
17	Species-(herb-)rich	13.5	29.7	33.7	7.4	20.1
-	Short grass (< 25mm high)	15.1	13.8	17.4	11.5	17.75
2	Therophyte zone/sparse vegetation	8.0	2.75	24.0	26.15	15.9
18b	Sheep-grazed	20.6	32.65	3.7	7.3	15.4
7	Maritime heath	0.7	10.2	39.1	7.4	13.8
10	Path(-side)	7.5	6.8	34.4	3.9	12.6
21	Cereal grains	10.3	9.55	5.5	18.3	11.3
4	Shallow earth	14.6	1.0	3.1	18.3	9.95
1b	Cliff-edge	3.2	0.9	12.7	19.7	9.7
1a	Cliff-top	4.5	0.2	9.0	20.5	9.3
-	Variable height grass	8.8	5.1	21.2	0.5	8.5
13	Permanent/old grassland	12.2	23.3	0.1	0.1	8.3
18d	Rabbit-grazed	0	0	33.0	1.1	8.1
18a	Cattle-grazed	11.6	16.55	1.6	1.85	7.5
14	Old-(semi-)improved grassland	11.1	0	0.3	1.8	6.4
8	Seabird-cliff flora	0.2	22.7	0	0	5.0
18c	Equine-grazed	2.9	14.0	0	0	3.8
-	Medium height grass (25-50mm)	8.7	2.4	1.0	3.0	3.8
9	Rocky outcrops	0.8	7.2	5.9	0	3.2
22e	Ruderal/neglected agriculture	9.25	3.5	0.1	0	3.1
12	Wall/Hedgebank	3.6	8.8	0	0.03	2.9
20	Rough-grazing	5.9	5.1	0.1	0	2.6
16	Stoney substrate	5.0	3.2	0.15	0	2.0
22c	Silage/hay aftermath	0	3.5	0	0.3	0.85
22?	Other agriculture	0	3.8	0	0	0.85
15	Drilled/reseeded/improved grass	0.2	0	0.4	1.8	0.8
19	Dung-feeding	1.9	0.3	0.5	0	0.7
-	Tall grass (> 50mm)	1.0	0	1.6	0.1	0.7
1d	Scree	0	0.1	1.35	0.1	0.4
18?	Unknown grazing	0.6	0	0	0	0.3
22d	Root crops/brassicas	0.1	0	0	0	0.02
	TOTAL PCMs	5618	4869	5240	6423	22150

Figure 4.7

Percentage of Chough feeding time (FCMs) spent in cliffs and unimproved habitats. Yearly values on left and winter values on right, including, for comparative purposes, the mean winter Cornish value from the Rame study (Appendix IV)



Year total



Winter (including Cornwall)

natural zone between inland agriculture and the natural cliffs (see Section 4.3.2). Choughs fed on sheep-grazed land for 15.4% of time, and on cattle-grazed land for 7.5%. In study areas W1 & W2, where there is an upland pastoral-based agriculture, these values increase to give 26.2% and 13.9% for sheep- and cattle-grazing respectively. At Strumble, grazing by all domestic livestock accounts for >60% of FCMs. Where plentiful and where the agriculture is more improved, as at Newgale-Solva, Choughs switch to rabbit-grazed swards (33% of FCMs *cf.* 3.7% and 1.6% for sheep- and cattle-grazed pasture respectively). Elsewhere, however, unlike the situation at Stackpole and on the islands of Skomer and Ramsey, where Chough populations might be faring slightly better, rabbits, and the effects of their grazing, were rarely apparent.

Time spent feeding within the cliff complex increases through the year from 64.7% in the winter to 87.2% in high summer (Table 4.6, Figure 4.7). During the winter at Mwnt-Cemaes, the cliffs were used for only 21.1% of feeding time, compared to 93.2% at Newgale-Solva; the regional mean of 64.7% is very close to that recorded in the preliminary Cornish study (*cf.* Figure 4.7; see Meyer 1990, Appendix IV). The onset of breeding at Mwnt-Cemaes resulted in a >40% increase in cliff usage; at Newgale-Solva and Marloes there were smaller increases, at Strumble there was a >30% decrease to 51.35%. The post-breeding season resulted in a consistently high cliff usage, ranging from 72.6% (Mwnt-Cemaes) to 96.1% (Marloes). For the year, there was a 35% difference in extremes: Newgale-Solva gave the highest cliff usage (92.9%: in no season was usage <90%), and Mwnt-Cemaes the lowest (57.8%).

Table 4.6 Time in FCMs with (%) observed spent feeding on cliffs

Study area	Season Winter	 Breeding	 Post-breeding	Year
W1/Mwnt-Cemaes	208 (21.1)	1930 (62.2)	1108 (72.6)	3246 (57.8)
W2/Strumble	2096 (81.8)	1118 (51.4)	115 (87.8)	3329 (68.4)
W3/Newgale-Solva	669 (93.2)	1649 (97.5)	2553 (90.2)	4871 (92.9)
W4/Marloes	1674 (57.5)	1891 (94.2)	1448 (96.1)	5013 (78.0)
Total FCMs on cliffs	4647 (64.7)	6588 (73.4)	5224 (87.2)	16459 (74.3)
Total FCMs	7177	8980	5993	22150

Figure 4.8 shows the biomes and principal habitat components which were allocated for each feeding observation, enabling the mean proportional observed feeding time (PFT) to be calculated. The end categories represent possible principal components of the habitat; tracing the dendrogram up by strata shows associated components for all feeding events. The dendrogram may be read rectangularly, *i.e.* horizontally (by hierarchical strata) or vertically (by biome section); alternatively, other groups may be taken (*e.g.* as defined by human activity) which cut across the rectangularity, for example, the half-shaded boxes in Figure 4.9 show all natural complex or natural zone (PFT=.555).

The PFT based on daily means for the major biomes, with seasonal variation, is shown in Table 4.7, because the data are not normally distributed, median values are also given. There is a good level of

Table 4.7 Mean proportion of feeding time (PFT) ±1 s.e. with median values per observational period (=N) spent in main biomes. Old grassland is here included as part of pastoral agriculture, see Table 4.8 for its inclusion as part of the cliff complex (see text for explanation)

Study area	Biome												
	Cliffs			Transitional			Pastoral			Arable			
	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	N
W1/Mwnt-Cemaes	.39	.15	.07	.17	.05	.04	.38	.23	.06	.05	.00	.04	37
W2/Strumble	.59	.63	.10	.13	.00	.06	.21	.00	.08	.07	.00	.06	17
W3/Newgale-Solva	.58	.63	.10	.36	.37	.08	.02	.00	.87	.04	.00	.03	17
W4/Marloes	.76	.81	.06	.11	.00	.04	.02	.00	.02	.13	.00	.05	25
K	10.05			11.63			33.32			8.01			
d.f.	3			3			3			3			
P	<0.05			<0.01			<0.001			<0.05			
Season													
Winter	.50	.53	.09	.07	.00	.03	.20	.00	.08	.23	.01	.07	20
Breeding	.55	.63	.05	.21	.06	.04	.24	.00	.05	.00	.00	.00	53
Post-breeding	.60	.81	.09	.22	.00	.07	.07	.00	.04	.11	.00	.06	23
K	1.52			5.45			3.96			24.74			
d.f.	2			2			2			2			
P	N.S.			N.S.			N.S.			<0.001			
Region	.56	.65	.04	.18	.03	.03	.19	.00	.03	.07	.00	.02	96

Kruskal-Wallis 1-way ANOVA test

Figure 4.8

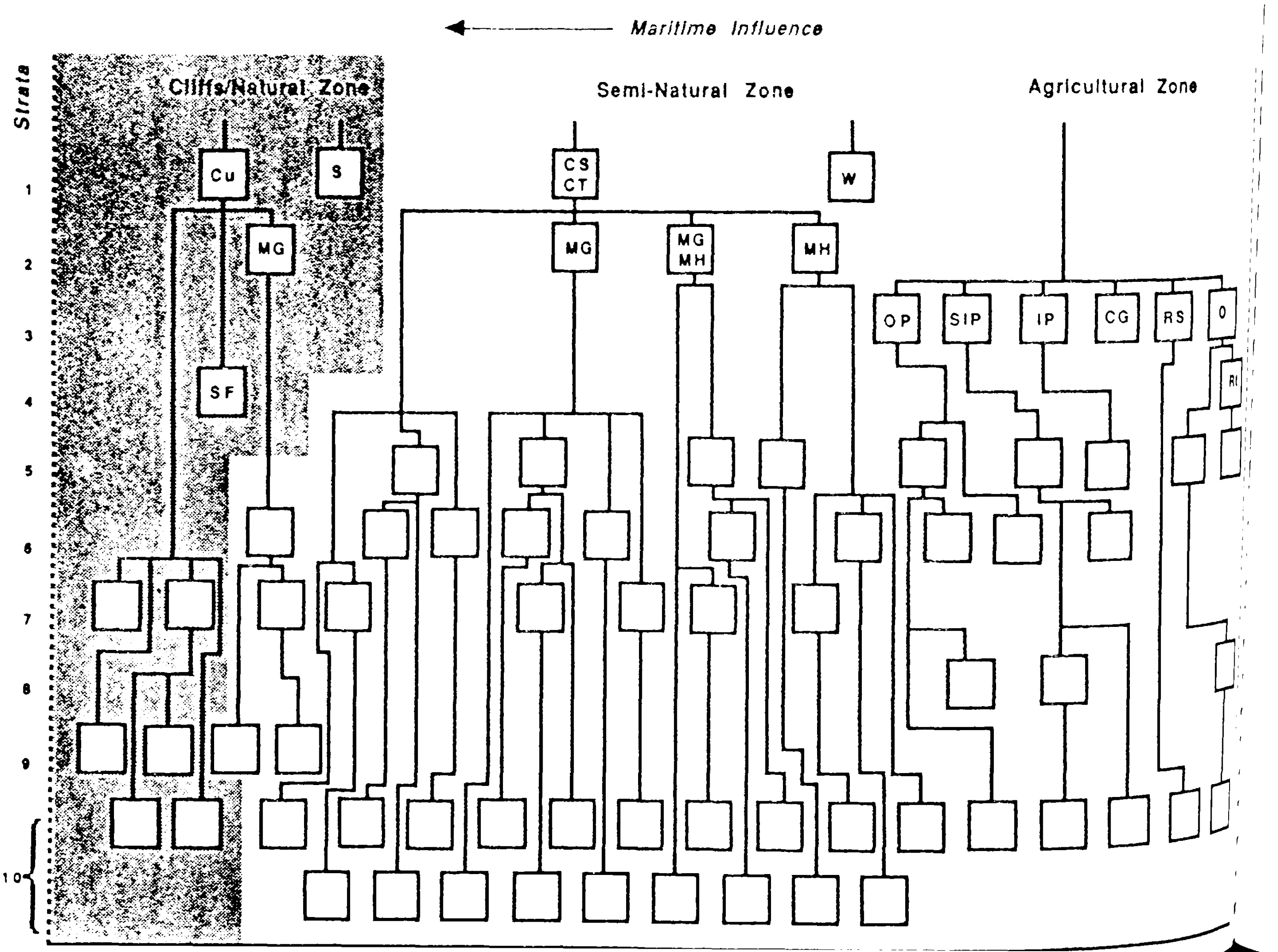
Dendrogram of principal feeding components, arranged rectangularly by vertical biome section and by horizontal hierarchical strata. Values are proportions of all feeding time (mean PFT) recorded during time dedicated to bird observation, and give probable principal components (end valued boxes) together with associated components, represented either by open boxes or valued boxes, where these values represent the principal (or end) components of other feeding incidents. The dendrogram should be read vertically from end box values to trace associate components

NB. Open boxes represent associate components which have no end or principal component value of their own

Key:

Biome section (zones):
C/N=Cliffs/natural; S-N=Semi-natural; A=Agricultural

Strata:
1 (Semi-)natural structure
2 (Semi-)natural vegetation type
3 Agricultural regimes
4 Seabird cliff flora (C/N); root crops/brassicas (A)
5 Dung
6 Path (-effect)
7 Rock-vegetation interface
8 Ruderal agriculture
9 Therophyte zone (effectively a sub-group of Stratum 10)
10 Exposed substrate


Maritime Influence
Strata
Cliffs/Natural Zone
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Agricultural Zone
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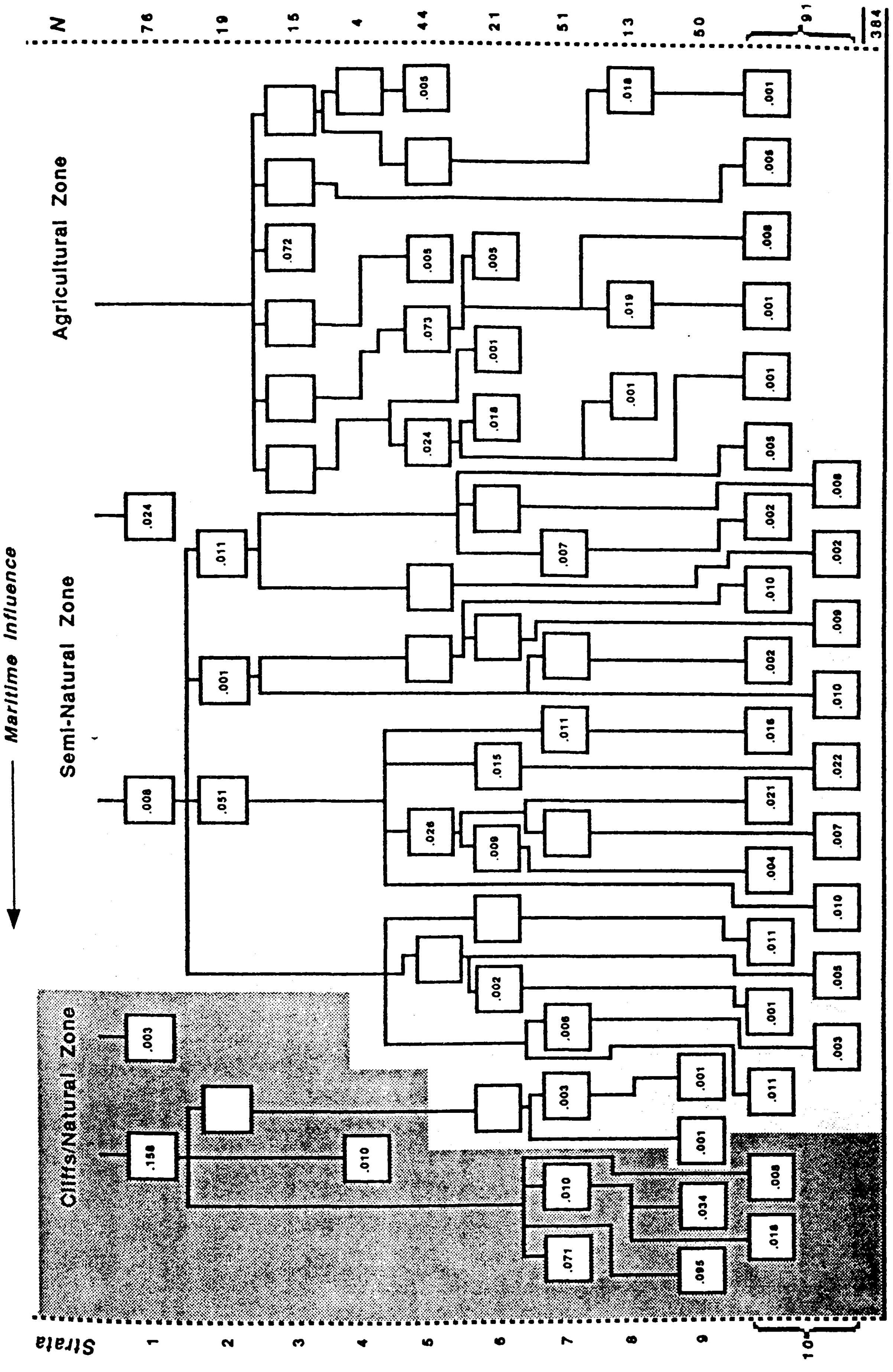
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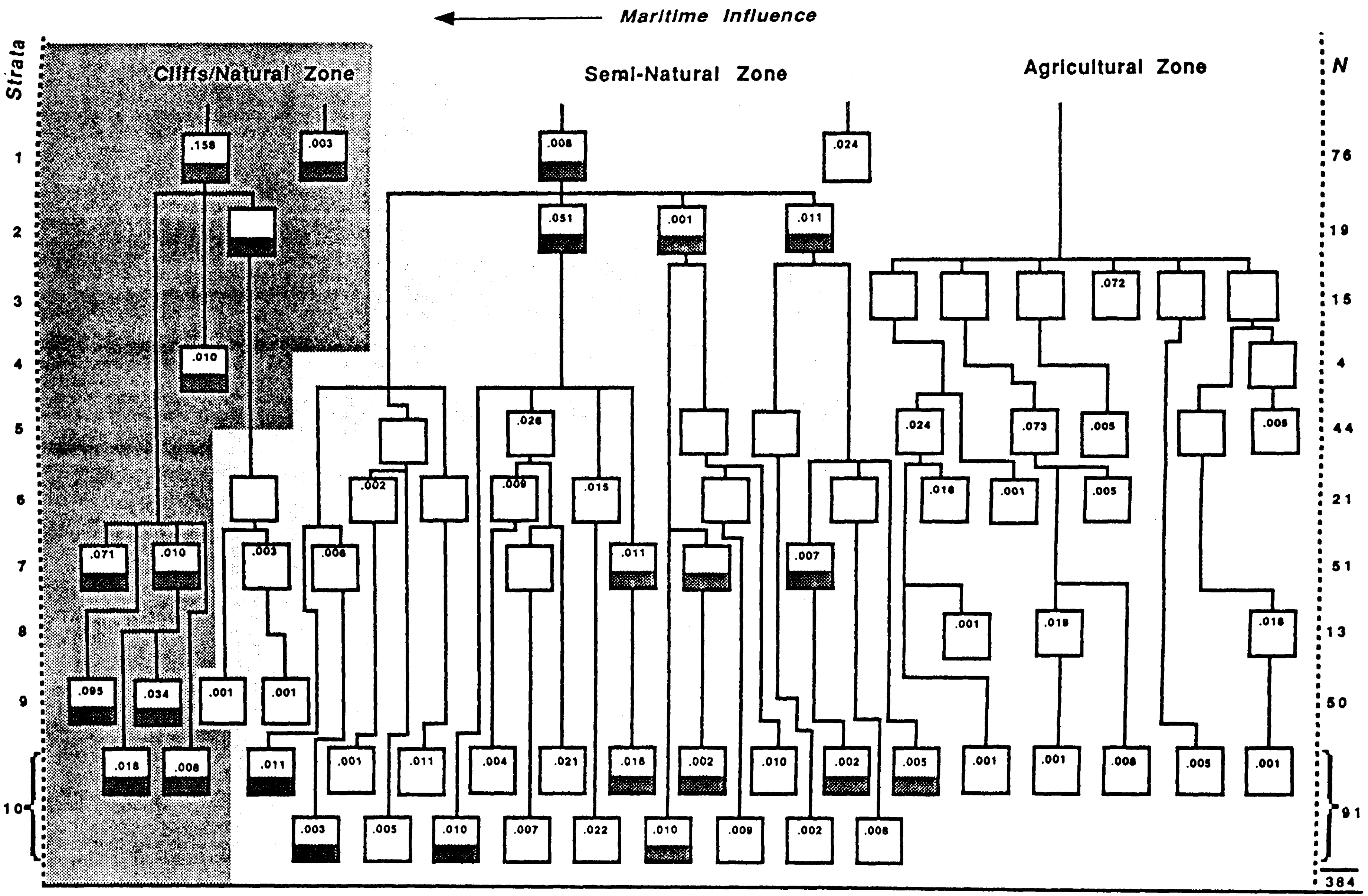
Figure 4.9

Figure 4.8 re-presented to show possibility of non-rectangular interpretation. In this case, the shaded boxes show an extended cliff complex: the non-human-influenced zone


Maritime Influence
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.026
.024
.073
.005
.005
.002
.009
.015
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.001
.005
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.010
.003
.006
.011
.007
.001
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.018
.095
.034
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.008
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.008

agreement between PFT and FCM analyses; for example, cliffs/natural: PFT=.55, FCMs=64.5%; cliff complex (cliffs + transitional/semi-natural): PFT=.73, FCMs=74.3%. Table 4.6 shows that usage, except at Mwnt-Cemaes during the winter, of the natural maritime cliffs never fell below half; the Mwnt-Cemaes low is probably explained by sympathetic agriculture and management (4.3.4), and is responsible for depressing the regional winter value and consequently also the annual value. Regional winter values, excluding Mwnt-Cemaes, show 71.7% cliff usage, only 1.7% below the breeding season regional use.

In PFT analysis, cliff usage differs significantly (Table 4.7), increasing southwards from PFT .39 at Mwnt-Cemaes to .76 at Marloes. There was no significant seasonal variation in cliff usage, neither was there significant seasonal variation in the use of pastoral agriculture but there was a very highly significant difference in pastoral usage between study areas; the relatively low cliff usage at Mwnt-Cemaes being offset by a higher degree usage of pasture, giving a 50:50 ratio (Table 4.7). An opposite situation applied at Newgale-Solva and Marloes, where improved agriculture reduced the PFT spent on pasture ($P<0.001$) and resulted in increased feeding time on the cliffs, and, in the case of Marloes, on arable land. When the usage of arable is assessed seasonally, there was a very high significance between zero PFT in the breeding season to a winter high of .23 ($P<0.001$; Table 4.7). Seasonality did not significantly affect usage of the other biomes.

The transitional semi-natural zone was used significantly more at Newgale-Solva (PFT .36) than anywhere else, in fact, more than twice as much ($P<0.01$; Table 4.7). Maritime grass on cliffslopes when grazed can grade into old or permanent pasture (*e.g.* 'U46', Table 4.2), whereupon it may be regarded as semi-natural and could legitimately be categorised as 'cliffs', 'semi-natural' or 'pastoral agriculture'. Table 4.8 gives the PFT for 'old permanent grassland' when extracted from modern agriculture, and also when regarded as an element of the natural cliffs, and as a component of an extended (semi-)natural cliff complex (*e.g.* with walls and human-influenced natural communities). It is immediately apparent from Table 4.8, that usage of old (-improved) grassland is very significantly greater in W1 and W2 to the north, than in study areas W3 and W4 to the south where agriculture is intensively improved ($P<0.001$); the reduced availability (see Section 4.3.3b) of rough-grazed permanent grassland in these study areas resulted in virtually zero usage (but see Section 6.4). Although mean usage of pastoral elements increases during the breeding season (falling off sharply immediately afterwards), there were no significant differences between the seasons (Table 4.8). However, when grassland is regarded as part of the natural cliff complex, the differences between study areas begin to disappear, although there is an insignificant increase in selection of cliff habitat in the two southern, more agriculturally improved areas. Results presented later on (Chapter 6) regarding foraging success, suggest that, while it was tempting above to use the expression 'increased dependence' or 'increased reliance', in place of 'increased selection', to have done so might have been misleading; similarly I stated earlier that it was 'reduced availability' which caused zero usage; behavioural observations will cause reappraisal of such interpretations (as discussed in Section 4.3.4).

It is also apparent from Table 4.8, that the entire (semi-) natural cliff complex, including walls and other semi-natural habitats, is exploited to a significantly very much greater extent outside the winter period ($P=0.001$), rising from PFT .59 in the winter to .87 after the breeding

Table 4.8 The selection of semi-/old-improved pasture, old/permanent grassland, and transitional semi-natural habitats by Choughs within the cliff complex. Expressed as the mean proportion of feeding time (PFT) ±1 s.e. with median values per observational period (=N)

	Biome												
	Old- or semi-improved pasture			Old grassland alone			Old grassland as part of the cliff complex			Entire cliff complex: cliffs, old grassland, and other semi-natural habitats			
Study area	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	N
W1/Mwnt-Cemaes	.21	.01	.05	.18	.06	.05	.57	.61	.06	.74	.99	.06	37
W2/Strumble	.13	.00	.08	.09	.00	.04	.67	.68	.10	.80	1.0	.11	17
W3/Newgale-Solva	.02	.00	.01	.00	.00	.00	.58	.63	.10	.94	1.0	.03	17
W4/Marloes	.00	.00	.00	.00	.00	.00	.74	.81	.06	.87	1.0	.06	25
K	25.31			33.07			2.92			6.40			
d.f.	3			3			3			3			
P	<0.001			<0.001			N.S.			N.S.			
SEASON													
Winter	.08	.00	.05	.06	.00	.03	.56	.64	.08	.59	.74	.09	20
Breeding	.15	.00	.04	.10	.00	.03	.65	.76	.05	.85	1.0	.04	53
Post-breeding	.03	.00	.03	.04	.00	.02	.65	.93	.09	.87	1.0	.06	23
K	5.18			1.00			1.62			13.40			
d.f.	2			2			2			2			
P	N.S.			N.S.			N.S.			0.001			
All	.11	.00	.03	.08	.00	.02	.64	.74	.04	.82	1.0	.03	96

Kruskal-Wallis 1-way ANOVA test

season. Seasonal sample sizes for individual study areas were small, but only during the breeding season was there significant differences between the study areas in the mean proportion of time spent feeding on the cliffs, increasing very significantly southwards, *i.e.* towards W4:

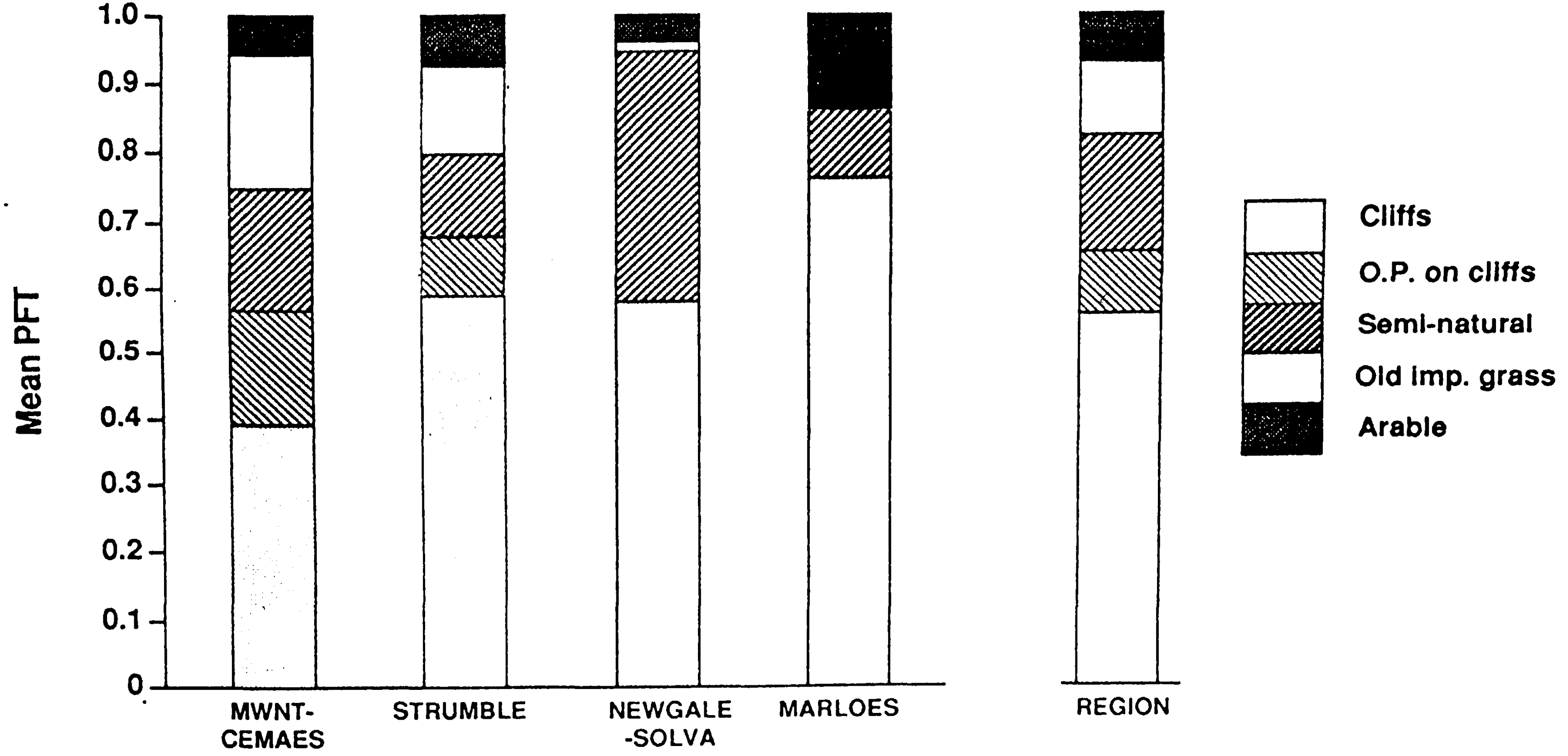
W4/Marloes PFT=1.0, median=1.0, ±1s.e.=.04, n=12
W3/Newgale-Solva PFT=.97, median=1.0, ±1s.e.=.03, n=10
W2/Strumble PFT=.67, median=.76, ±1s.e.=.11, n=11
W1/Mwnt-Cemaes PFT=.57, median=.72, ±1s.e.=.09, n=20
Kruskal-Wallis 1-way ANOVA: $K = 18.58$, d.f.3, $P<0.001$

Across the region, the (semi-)natural cliff complex represented a mean value of .82, the balance comprising arable (Table 4.7) and semi-improved agriculture (Table 4.8). Only at Mwnt-Cemaes did usage fall below 75% (.74), while at Newgale-Solva, it increased to .94. Figure 4.10 displays the increase in cliff usage in the study areas southwards (possibly representing increasing cliff quality) and the compensatory roles played by arable land, and the transitional categories of rough-grazed cliff grassland, other semi-natural habitats and old improved pasture.

The most important habitat components of feeding sites (shown in Table 4.5) were also tested for variance between study areas and seasons. The component appearing most frequently in Chough feeding sites was exposed earth: involving at least 8981 FCMs (40.5%), confirming Bullock's theory, tentatively advanced in his thesis (1980) that bare earth was especially important. It may be theorised that this percentage is actually even higher because the exposed substrate element is partly linked to usage of the cliffs (accommodating the majority of feeding sites which could not be examined in detail). In study areas W3 & W4, where there was a common cliff usage of 64.8%, the exposed substrate value was 58.2%, in study

Figure 4.10

Time (mean PFT per observational period) spent in different habitat categories: cliffs, rough-grazed cliff grassland (O.P. on cliffs), semi-natural habitats, old-improved grassland, and arable. Data from Table 4.7 (cliffs, arable, semi-natural (transitional) habitats), and Table 4.8 (old pasture on cliffs (=rough grazing), and old-/semi-improved grassland)


Mean PFT
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
MWNT-CEMAES
STRUMBLE
NEWGALE -SOLVA
MARLOES
REGION
Cliffs
O.P. on cliffs
Semi-natural
Old imp. grass
Arable

areas W1 & W2, where cliff usage was reduced to 53.8%, usage of exposed substrate fell to 20.9% (Table 4.5). As the principal component (or end category), the regional mean PFT was .33, ranging from a low of .01 in the agricultural biome to .21 on the cliffs (Figure 4.11). There was a significant difference (Table 4.9) in overall usage of exposed substrate between study areas, caused by a high variance within the cliff biome (PFT .09 - .42; $P<0,01$), and, again overall, usage was significantly lowest in winter and highest in the breeding season ($P<0.05$). In Newgale-Solva and Marloes combined, the two areas where cliffs were most used (Table 4.6), the mean PFT was .34 (±1s.e. .05).

If habitats of unknown configuration are excluded from the analysis, the usage of exposed substrate could be expected to increase. It may be safely assumed that bare earth also supported feeding incidents in these habitats (primarily the inaccessible cliffs), and the maximum potential values are as shown in Figure 4.12. It is apparent that exposed substrate could well support more than three quarters of all feeding time within the natural cliff complex.

Short-grazed grassland, often said to be the main habitat requirement for Choughs, was involved in only 17.75% (3932) of FCMs regionally, and 43.6% of these were on open swards, *i.e.* mutually inclusive with bare earth (Table 4.5): thin/sparse grass and so-called 'sheep-bare' (Owen 1985). Approximately 15% of FCMs were associated with sheep-grazing, and 12% of FCMs (2653) were 'sheep-bare' linking exposed earth with sheep-grazed grass <25mm high; this represents 77.8% of all time associated with sheep-grazing, and 29.5% of all time associated with exposed earth. Feeding bouts involving exposed earth and sheep-grazed vegetation >25mm high or of variable height occurred in a further 450 FCMs. Over 20% of FCMs occurred on species-rich grassland (not necessarily sheep-grazed).

Table 4.9 Usage of exposed substrate in principal biomes. Expressed as the mean proportion of feeding time (PFT) ±1 s.e. with median values per observational period (=N)

	Biome												
	Cliffs			Semi-natural			Agricultural			All			
Study area	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	N
W1/Mwnt-Cemaes	.17	.04	.04	.10	.00	.02	.02	.00	.02	.29	.17	.05	37
W2/Strumble	.09	.00	.03	.11	.00	.04	.00	.00	.00	.20	.00	.06	17
W3/Newgale-Solva	.42	.43	.08	.17	.00	.07	.00	.00	.00	.59	.49	.08	17
W4/Marloes	.25	.26	.05	.09	.00	.04	.02	.00	.02	.32	.32	.06	25
K	15.39			4.33			1.51			12.52			
d.f.	3			3			3			3			
P	<0.01			N.S.			N.S.			<0.01			
SEASON													
Winter	.14	.00	.06	.04	.00	.02	.02	.00	.02	.20	.00	.06	20
Breeding	.24	.18	.03	.18	.00	.04	.02	.00	.01	.44	.29	.05	53
Post-breeding	.25	.10	.07	.13	.00	.06	.00	.00	.00	.38	.22	.07	23
K	6.09			9.29			2.43			9.99			
d.f.	2			2			2			2			
P	<0.05			<0.01			N.S.			<0.01			
Region	.21	.10	.03	.11	.00	.02	.01	.00	.01	.33	.21	.03	96

Kruskal-Wallis 1-way ANOVA test

Figure 4.11

Usage of exposed substrate. Percentage of PFT (overall $\bar{x}$ .33) ±1 s.e. spent in the principal biomes;

N = observational periods

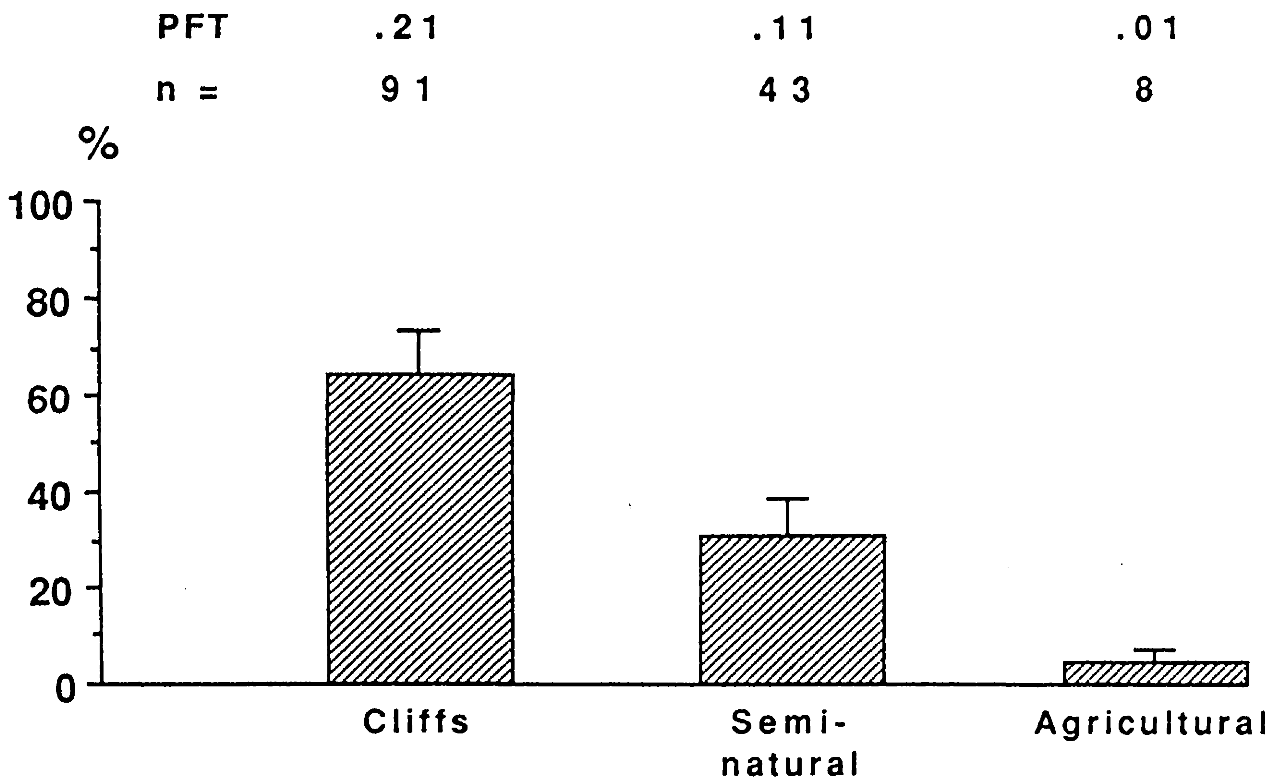
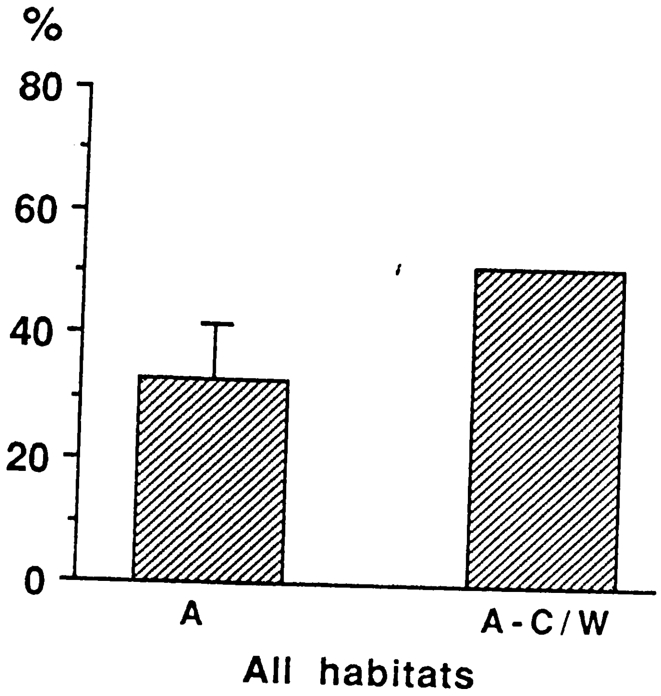

PFT
.21
.11
.01
n =
91
43
8
%
100
80
60
40
20
0
Cliffs
Semi-natural
Agricultural

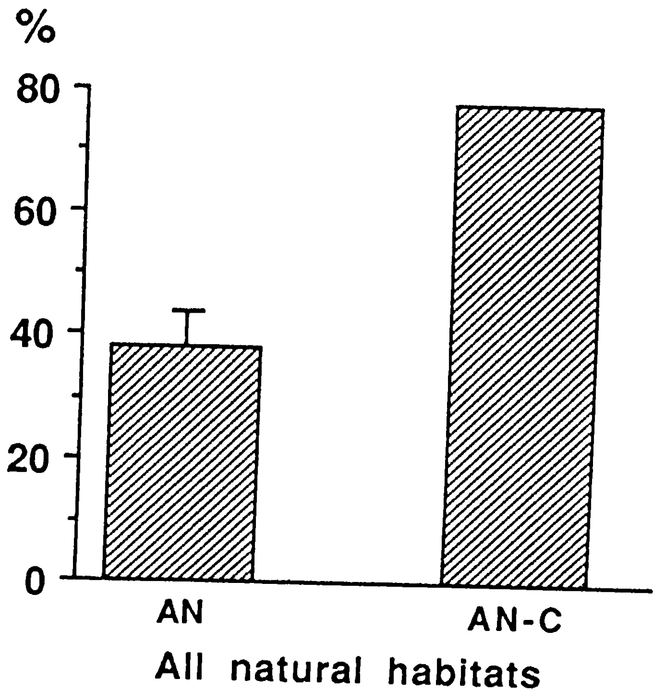
Figure 4.12

Usage of exposed substrate (% of mean PFT per observational period, ±1 s.e., N = 96) and hypothesised maximum values if habitats of unknown configuration supported exposed substrate feeding (based on data given in Figure 4.8 and Table 4.9)

Key:

A	all exposed substrate (overall minimum value)
A+C/W	all biomes excluding unspecified records, *i.e.* unspecified clifflands and walls (giving overall maximum *potential*)
AN	all natural habitats (minimum value)
AN+C	all natural habitats excluding unspecified clifflands (giving maximum *potential* within natural biome)


%
80
60
40
20
0
A
A-C/W
All habitats


%
80
60
40
20
0
AN
AN-C
All natural habitats

The exposed earth specifically associated with therophyte communities supported almost 16% of FCMs (3524) (see also Section 4.4). Maritime grassland was associated with 23.8%, and 28% were concentrated at rock/earth-vegetation interfaces which provides a fissure exploitable by both Choughs and invertebrates (Table 4.5).

Habitat shaped by mound-building ants was present and identifiable in all study areas. *Lasius flavus*, in particular, is able to alter substantially the physical constituents and topography of grassland, and once established can even survive the spread of vegetation (Wallwork 1976). Since the ants themselves were the attractant rather than the habitat type *per se*, it was decided to include certain ant biotopes as categories of Chough feeding habitats.

Ants were preyed upon by Choughs in all study areas (5.3.1). Habitat shaped by ants had a mean usage of >20%, concentrated into the two warm weather seasons. The values presented in Table 4.5, suggest that ants are less preferred in pastoral areas: study areas W1 & W2 = 12% and 4.9% *cf.* study areas W3 & W4 = 46.9% and 21.5% respectively, but this could also reflect the spatial distribution of the ants themselves (4.3.4) and inter-specific behavioural differences (*e.g.* not all ants build mounds). Even though ant-formed habitats were utilised in all study areas analysis showed significant variance both by site, with ant habitats being used most in Newgale-Solva, and by season (Table 4.10); the latter due to the increased summer activity. Observations indicate that, if available, Choughs can prey on ants at all times of the year.

Dung is an important resource *at times*; more than one quarter of all PFT (.26, median .00, ±1 s.e. .04, n = 96) was associated with dung, although

Table 4.10 Mean proportion of time (PFT) ±1 s.e. with median values per observational period (=N) spent feeding in ant-created habitats

Study area	PFT	med.	s.e.	N	*K*	d.f.	*P*
W1/Mwnt-Cemaes	.14	.00	.05	37			
W2/Strumble	.12	.00	.05	17			
W3/Newgale-Solva	.42	.49	.08	17			
W4/Marloes	.23	.04	.06	25	12.56	3	.0057
Season							
Winter	.03	.00	.03	20			
Breeding	.22	.02	.04	53			
Post-breeding	.34	.22	.08	23	13.86	2	.0010
Region	.21	.00	.03	96			

Kruskal-Wallis 1-way ANOVA test

very little actual dung-feeding was observed: only for 120 (2.7%) of 3613 dung associated FCMs (Table 4.5). The majority of time was spent in dung-rich habitats, with the birds possibly feeding on dung fauna made available by the grazed conditions. In a later chapter, the importance of dung fauna is discussed. On aggregated FCM data from Table 4.5, dung-feeding was commonest in the north (89%), with 72% at Mwnt-Cemaes; as a mean proportion of feeding time per day, feeding associated with dung resulted in:

W1/Mwnt-Cemaes	PFT=.43, median=.29, ±1s.e.=.06, n=37
W2/Strumble	PFT=.26, median=.00, ±1s.e.=.09, n=17
W3/Newgale-Solva	PFT=.24, median=.00, ±1s.e.=.08, n=17
W4/Marloes	PFT=.04, median=.00, ±1s.e.=.04, n=25

Kruskal-Wallis 1-way ANOVA showed a very high significance between the northern and southern study areas: K=27.31, d.f. 3, $P<0.001$. There was no significant seasonal difference (K=2.52, d.f. 2). Environments enriched rabbit dung are included; however there is very little similarity between the invertebrate fauna of rabbit dung and that of, say, cow dung, and this will affect and, to some extent, govern Chough diet.

4.3.3b THE EFFECT OF HABITAT AVAILABILITY

It is self-evident that the availability of habitat will affect its selection. It was necessary to redefine habitat by biotope rather than the components given in the preceding section, which are not measurable accurately due to their small size (sometimes presumably visible only to Choughs), pocketed distribution, physiographical or temporal complexity or a combination of these factors. The areas of the defined biotopes comprising the study areas are given in Table 4.11. Cliffland values include some estimation due to complex coastal physiography. Cemaes Head

Table 4.11 Availability (ha) of habitat biotopes per study area and region. The Mwnt-Cemaes Study Area (W1) values are also given per sub-area: W1A=Mwnt, W1B=Cemaes, W2=Strumble, W3=Newgale-Solva, W4=Marloes

Sub-area of W1				Biotope	Study Area								Region	
W1A		W1B			W1		W2		W3		W4			
ha	%	ha	%		ha	%	ha	%	ha	%	ha	%	ha	%
2	2.0	6	4.0	Available cliff	8	3.0	10	4.0	8	6.0	28	9.0	54	6.0
7	8.0	9	6.0	Old grass/(semi-) natural, short/grazed	16	6.5	57	22.0	26	19.0	24	8.0	123	13.0
3	3.0	42	27.0	Old- (semi-) improved pasture	45	18.5	0	0	0	0	9	3.0	54	6.0
34	38.0	31	20.0	Improved pasture	65	26.5	64	25.0	27	19.0	84	27.0	240	25.0
9	10.0	9	6.0	Arable	18	7.5	4	1.5	22	16.0	67	22.0	111	12.0
29	33.0	49	31.5	Scrub/long vegetation	78	32.0	122	47.0	56	40.0	83	27.0	339	36.0
0	0	7	4.5	Other	7	3.0	1	0.	0	0	10	3.0	18	2.0
5	6.0	2	1.0	Homesteads	7	3.0	0	0	0	0	4	1.0	11	1.0
89		155		Total hectares	244		258		139		309		950	

and Newgale-Solva had 30-40% habitat yielding access to natural or semi-natural habitats.

In Cornwall, there was a weak negative correlation between availability and usage (r_s = -0.295, N.S; Meyer 1990, see Appendix IV). From data presented in Tables 4.12 and 4.13, usage is correlated with availability (see Figures 4.13 and 4.14). A relationship similar to the Cornish data is found: r_s = -0.125. At Mwnt-Cemaes, an increase in the availability of semi-natural grassland possibly causes a reciprocal increase in usage and a decrease in cliff usage, giving a weak correlation coefficient ($P<0.10$; Figure 4.13). At Strumble, the Choughs switch to an increased availability of old grassland. At Marloes, increased arable land, at the expense of old pasture, is exploited and reflected by an increase of cereal in the diet (Chapter 5). Most marked is the heavy usage made in all study areas of the small amount of available cliff habitat: over the region, this amounted to about 5% of cliff habitat supporting nearly 70% of Chough feeding-time (*cf.* Figure 4.10), and the importance of habitat quality, as opposed to quantity, introduced in the discussion below, is established in Chapter 6. The absence of significant correlations between availability and usage suggests that the Choughs are being selective in their choice of feeding habitat.

4.3.4. DISCUSSION

Variation in habitat selection across the region validated the decision to choose a range of study areas. The component data in Table 4.5 provide a means of stringing together habitat variables in order to help create suitable habitat-types in management programmes (Chapter 7). Figures 4.8

Table 4.12 Usage of habitat biotopes per study area and region. Time in FCMs and percentages per column. The Mwnt-Cemaes Study Area (W1) values are also given per sub-area on the left: W1A=Mwnt, W1B=Cemaes, W2=Strumble, W3=Newgale-Solva, W4=Marloes

Sub-area of W1				Biotope	Study Area								Region	
W1A		W1B			W1		W2		W3		W4			
FCMs	%	FCMs	%		FCMs	%	FCMs	%	FCMs	%	FCMs	%	FCMs	%
315	65.6	3024	58.9	Available cliff	3339	59.4	2664	54.7	4218	80.5	4927	76.7	15148	68.4
32	6.7	627	12.2	Old grass/(semi-) natural, short/grazed	659	11.7	1568	32.2	610	11.6	87	1.3	2924	13.2
106	22.1	342	6.7	Old- (semi-) improved pasture	448	8.0	0	0	18	0.3	113	1.8	579	2.6
0	0	12	0.2	Improved pasture	12	0.2	0	0	21	0.4	113	1.8	146	0.6
0	0	578	11.3	Arable	578	10.3	465	9.6	286	5.5	1175	18.3	2504	11.3
27	5.6	31	0.4	Scrub/long vegetation	58	1.0	0	0	83	1.6	8	0.1	149	0.7
0	0	524	9.5	Other	524	9.5	172	3.5	4	0.1	0	0	700	3.2
480		5138		Total FCMs	5618		4869		5240		6423		22150	

Table 4.13 Percentages of available habitat (AH) and usage (U) measured in FCMs, for the 4 Welsh study areas and region.
Key: W1=Mwnt-Cemaes, W2=Strumble, W3=Newgale-Solva, W4=Marloes
C = Available cliffs; OP = Old pasture; A = Arable (cereal grains); OIP = Old-improved pasture; R = Ruderal; S = Scrub; IP = Improved pasture; O = Other.
NB. Any % shortfall in habitat availability is accounted for by dwellings etc (*ie.* non-habitat).

	C		OP		A		OIP		R		S		IP		O	
Area	AH	U	AH	U	AH	U	AH	U	AH	U	AH	U	AH	U	AH	U
W1	3.0	59.4	6.5	11.7	7.5	10.3	18.5	8.0	2.8	9.5	32.2	1.5	26.4	0.2	0^*	0.1
W2	3.9	54.7	21.7	32.2	1.6	9.6	0	0	0.4	3.5	47.1	0	25.3	0	0	0
W3	3.9	80.9	18.5	11.2	15.9	5.5	0^*	0.3	0^*	0.1	42.1	1.6	19.6	0.4	0	0
W4	8.9	76.7	7.8	1.3	21.7	18.3	3.1	1.8	0	0	27.1	0.1	26.8	1.8	3.2	0
All	5.3	68.5	12.8	13.1	11.7	11.3	5.7	2.6	0.8	3.1	36.1	0.7	25.2	0.7	1.1	0

NB. * = <0.1

Figure 4.13

Relationship of usage by Choughs (%FCMs) and availability of habitats per study area. Area W1 (Mwnt-Cemaes) is shown with disaggregated values (see also Section 4.3.5)

Spearman rank correlation coefficients for study areas:

Mwnt-Cemaes $r_s = -0.750$, $P<0.10$, n=7

Strumble $r_s = -0.686$, N.S., n=6

Newgale-Solva $r_s = -0.500$, N.S., n=5

Marloes $r_s = -0.098$, N.S., n=7

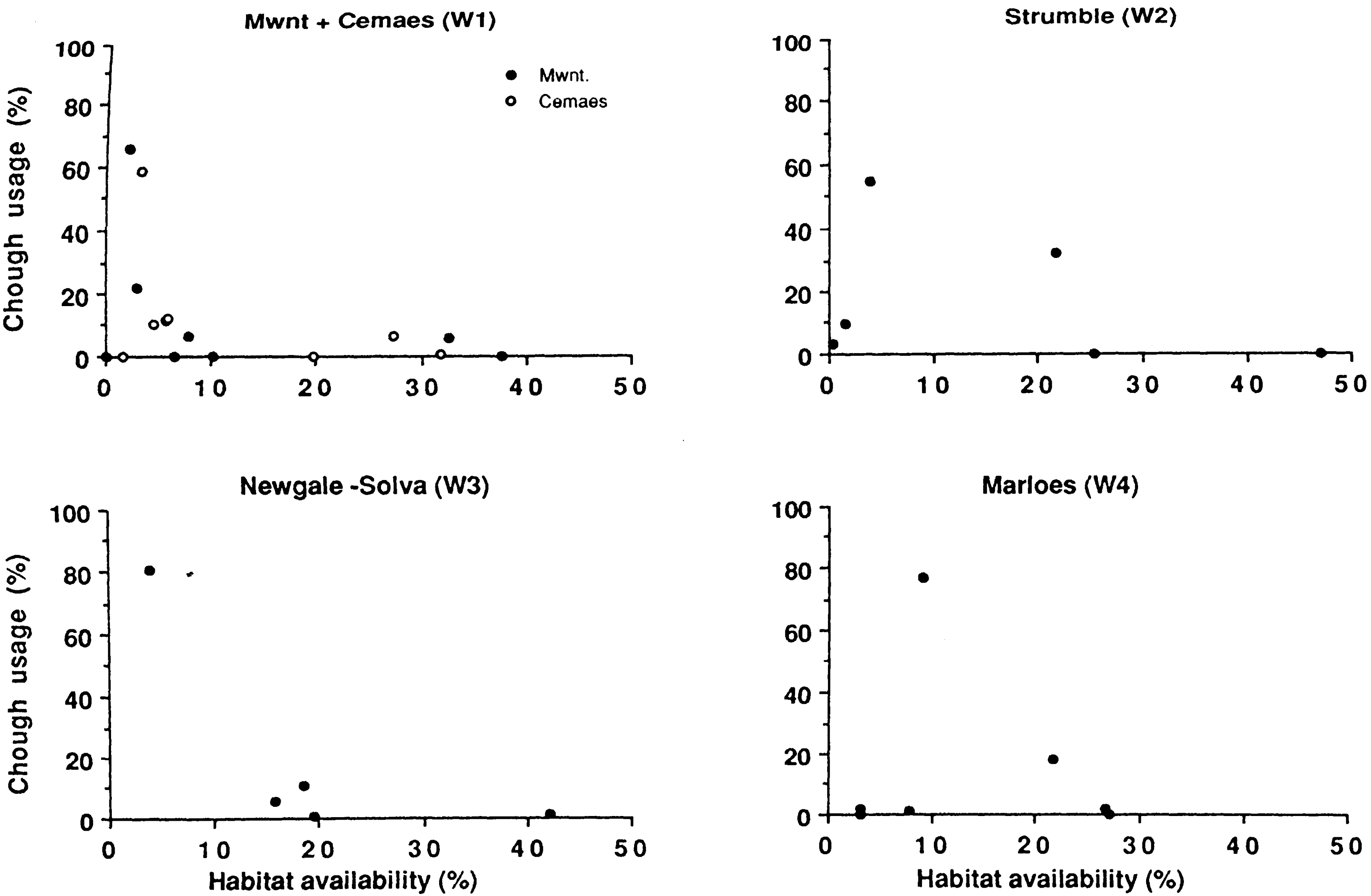
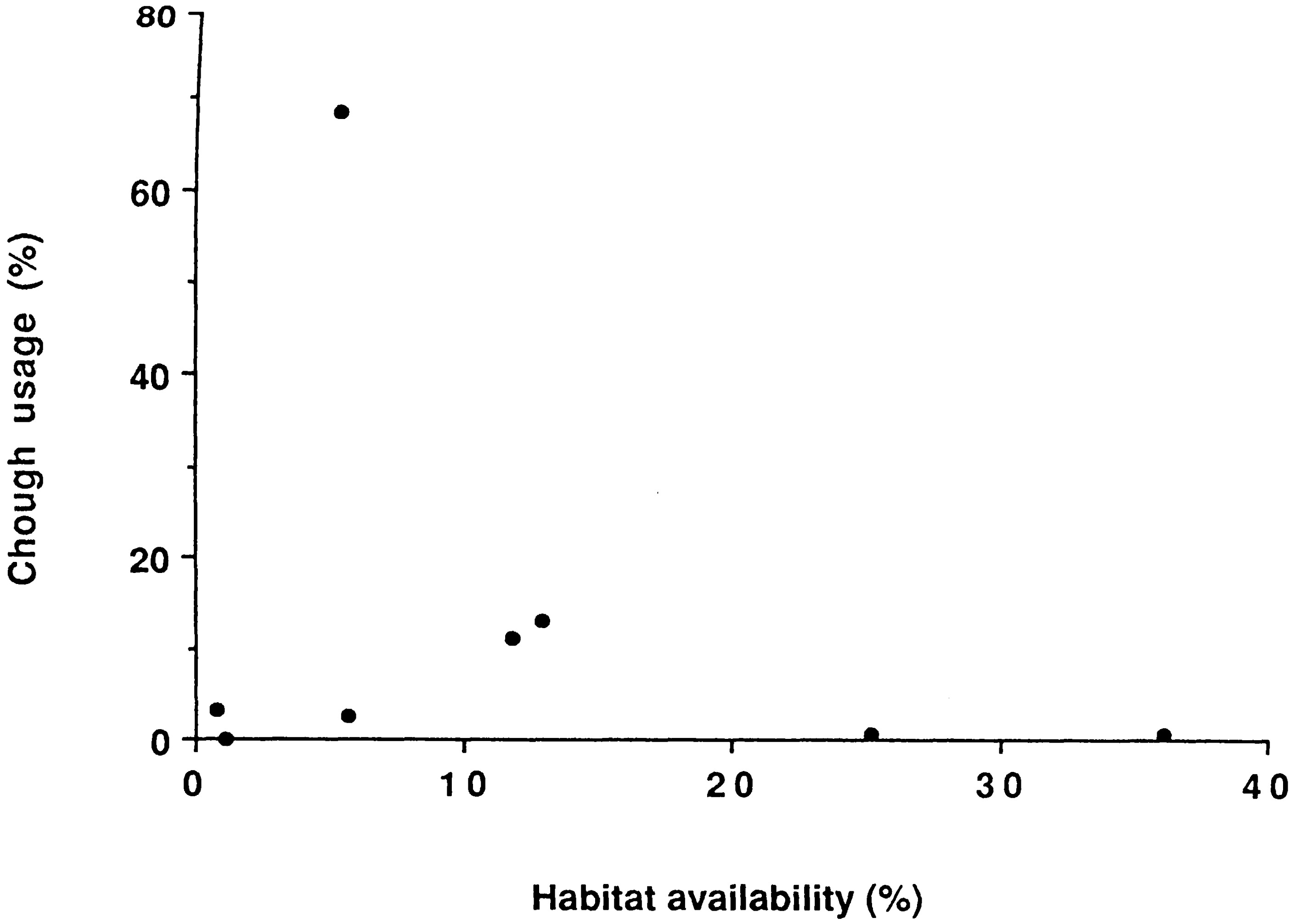

Mwnt + Cemaes (W1)
● Mwnt.
○ Cemaes
Strumble (W2)
Newgale -Solva (W3)
Marloes (W4)
Chough usage (%)
Habitat availability (%)
100
80
60
40
20
0
0
10
20
30
40
50

Figure 4.14

Relationship of usage by Choughs (%FCMs) and availability of habitats for aggregated study areas (=region)


80
60
40
20
0
Chough usage (%)
0
10
20
30
40
Habitat availability (%)

& 4.9 shows how the major components combine in Chough foraging patterns.

Cliffs are shown to be of major importance (Table 4.7 and Figure 4.10), and depending on where the line is drawn between natural and semi-natural habitats, this can increase still further. For example, if rough grazing on cliffs is included within the cliff complex (valid in view of its extent on cliffs and headlands in historic time (3.4.6e)), the difference between the study areas shown in Table 4.7 loses its significance, and the mean PFT increases to .64 within a decreased range (.57 - .74) (Table 4.8). When all semi-natural habitats are incorporated, the mean usage increases to .82, and it is possible to conclude that Choughs will use the transitional zone between the wild cliffs and the agricultural hinterland extensively when available, such as at Mwnt-Cemaes (Figure 4.10). Where this is not available to the same extent, such as at Marloes, there is an absolute requirement for high-grade cliffs. If these do exist, as indeed at Marloes, any agricultural short-comings are made irrelevant. The importance of the natural cliffs is underlined by investigations into foraging economics described in Chapter 6.

The importance of bare earth, within (semi-)natural vegetation mosaics, is clearly demonstrated. Table 4.9 shows how usage of this decreases from a mean PFT .21 in natural clifflands to .01 in agricultural land where the substrate is considerably more disturbed by human activity (mechanical and chemical) to the inevitable detriment of invertebrate communities (Wallwork 1976). The semi-natural zone (a 'mid-range' between natural and agricultural habitats), supports a midpoint PFT of .11 (*i.e.* between .21 and .01). There is a significant difference in usage of exposed substrate across the site range ($P<0.01$; Table 4.9), which was affected by availability and season, with usage lowest in the winter and increasing in the summer.

Usage of cliffland within the region is PFT .56 (Table 4.7). The lower usage at Mwnt-Cemaes (.39) is probably explained by a combination of relatively poor quality cliffs, and the special management within the Cemaes Head nature reserve and on the adjacent farmland in an initiative project designed by the NCC and Pembrokeshire Coast National Park explicitly to improve the habitat for Choughs. Elsewhere, usage of the cliffs *per se* ranges from mean PFT .58 to .76, which implies that unsuitable agriculture 'forces' an increased dependence on cliffs, although evidence presented in Chapter 6 suggests that high quality cliffland is preferentially selected over even Chough-friendly pastoral agriculture. The more improved the agriculture, the higher the dependence on cliffs (see also Chapter 5.4), resulting in the high value recorded at Marloes - the most agriculturally improved study area.

Table 4.14 Rank order of exclusive feeding habitat strata from Figure 4.8 with corresponding mean PFT

Rank	Stratum	PFT
1	Exposed substrate + therophyte communities	.331
2	Major unqualified biomes (mainly cliffs and walls)	.193
3	Dung	.133
4	Rock-vegetation interface	.108
5	Cereal grain	.072
6	Maritime grass and heath	.063
7	Paths	.050
8	Ruderal/atypical agriculture	.038
9	Seabird cliff vegetation	.010

Table 4.14 ranks the feeding habitats which were shown in hierarchical strata in Figure 4.8. The unspecified clifflands and walls (which provide a unique combination, in varying proportions, of natural, semi-

natural and agricultural components within a discrete unit) are ranked 2, but the second most important specific component is dung; it may often be the primary attractant when found in combination with other components, and, therefore, its importance is probably greater than intimated by a mean PFT of .133 (*cf.* associated mean PFT=.26, see p. 90).

Two of the commonest ant prey species, *Lasius flavus* and *L. niger*, generally inhabit exposed sites with sparse vegetation and little shade (Pontin 1961, 1963). Permanent pasture can encourage stable populations and, once established, *L. flavus*, by building mounds which rise above the level of the sward and altering the local topography, can even survive the cessation of grazing, but generally ants are reduced by the disturbance caused by large herbivores, and this is particularly true of *L. niger*, which builds loose mounds (Wallwork 1976). In Chapter 5, direct evidence of ant predation is examined but it is clear from the Choughs' selection of habitat that ants were heavily preyed on, confirming Cowdy's (1973) observations on Ramsey Island, especially at Newgale-Solva, where 46.9% of FCMs occurred in habitat influenced by mound-building species, all of these within the cliff region. Although, as would be expected from life-studies of ants, ant predation is highest in the summer, ants are taken throughout the year (Section 5.4).

The data presented in Table 4.5 and the multi-componental structure of Chough habitat, introduced in Section 4.3.1, reveal the physiography of Chough habitat. At Newgale-Solva, for example, it suggests quite accurately an environment characterised by grass-clothed cliffs, and retained in an open condition not by domestic livestock so much as by paths, rocky outcrops, rabbit-grazing, as well as ant activity.

4.4 THE BOTANY OF CHOUGH FEEDING SITES

4.4.1 INTRODUCTION

To define the structure of Chough feeding habitats even more precisely than was attempted in the component analysis based on the data given in Table 4.5, the accessible key Chough feeding sites were identified (those which supported >10 observed events) and a detailed botanical examination of these was undertaken in which species and cover composition were scored in order to relate the profiles to communities recognised within the National Vegetation Classification (NVC) (Rodwell 1982, Evans *et al.* 1989). It was hoped from this approach to produce botanical profiles which could be used as a guide to optimality of Chough feeding sites. Some quadrats were also surveyed in Cornwall for comparative purposes.

4.4.2 METHODS

In Wales, 58 key sites which were accessible and had supported >10 feeding events during regular bird observation, were identified (see Appendix VIII); of these, 52 were within the four main study areas (W1-W4), the remaining 6 were located at Stackpole NNR in south Pembrokeshire from information supplied by the NCC. Field botany is best understood in terms of plant communities (Tansley 1954), and it was intended to try and fit Chough feeding sites to the standard NVC, which is based on such communities. However, it was quickly apparent during survey work that Choughs do not select feeding sites from national botanical criteria! Many of the sites fell at the edges of recognised botanical communities or within ecotones. Interpretation by botanical community alone was, therefore, not sufficient, and recourse was made to species aggregations and their percentage cover ratios in order to construct profiles.

In July 1989, all species occurring within 2x2m quadrats, positioned at exact feeding points and initially ignoring botanical considerations, were assessed on the Domin range (Domin 1923, Shimwell 1971) of abundance (Table 4.15). Other 'cover types' were scored similarly: 'exposed substrate' (*ie*. how much of the quadrat was 'covered' by bare earth); 'dung' - identified to species; 'rock' (bedrock or large stones unable to be moved by birds); and 'stones' (loose/movable stones). The other variables recorded were: aspect, altitude, slope, soil-depth, and the homogeneous area of stand of which each quadrat was representative. As soon as possible afterwards (August 1989) in order to make the results as comparable as possible, 15 quadrats were also examined in Cornwall. At Rame (Chapter 8), a strategy similar to that employed in Wales was adopted; elsewhere, in the absence of present-day Chough evidence, representative samples in ex-Chough areas were taken, in stands which

Table 4.15 The Domin scale for scoring abundancy or percentage cover in 2x2m quadrats

Scale	Estimated cover
10	91 - 100
9	76 - 90
8	51 - 75
7	34 - 50
6	26 - 33
5	11 - 25
4	4 - 11
3	1 - 4 (frequent but low cover)
2	1 - 4 (occasional)
1	1 - 4 (rare - 1 or 2 individuals)

resembled the Welsh sites. These were: on the north coast, at Pentire Head (location #30 Figure 3.2; near the ancient Pentireglaze site (2.3.3) and at Beacon Cove (#27; the last Cornish site - see Figure 7.2); in West Penwith at Zennor (#19) and Gwennap Head (#14); and Predannack cliffs on the Lizard (#9; 2.3.3).

4.4.3 RESULTS

One hundred and nineteen plant species were recorded from 58 quadrats in Wales, and 44 from 15 quadrats in Cornwall. All those appearing in >10% (>5) of the Welsh quadrats are ranked in Table 4.16, with the 5 supplementary cover-types interpolated as appropriate. The dominant NVC type describing the Chough feeding sites is MC5 (*Armeria maritima - Cerastium diffusum* ssp. *diffusum* maritime therophyte community (Table 4.1); comparison of the distributions of this and present-day Chough distribution (Figure 4.15 *cf*. Figure 1.2) or, more closely still, distribution in recent historic times within Scotland, Wales and England, show remarkable affinity (the Isle of Man has not as yet received equivalent observer effort). It can be seen, from Table 4.16, that the two annual 'hair-grasses' (*Aira praecox* and *A. caryophyllea*) represent 58.6% and 39.7% presence in all quadrats. The *Aira praecox* sub-community of MC5, which is widespread particularly around the Mull of Galloway (NCC 1989), itself an important historic site for the Chough in Scotland until the early part of this century (Baxter & Rintoul 1953), was the dominant sub-type.

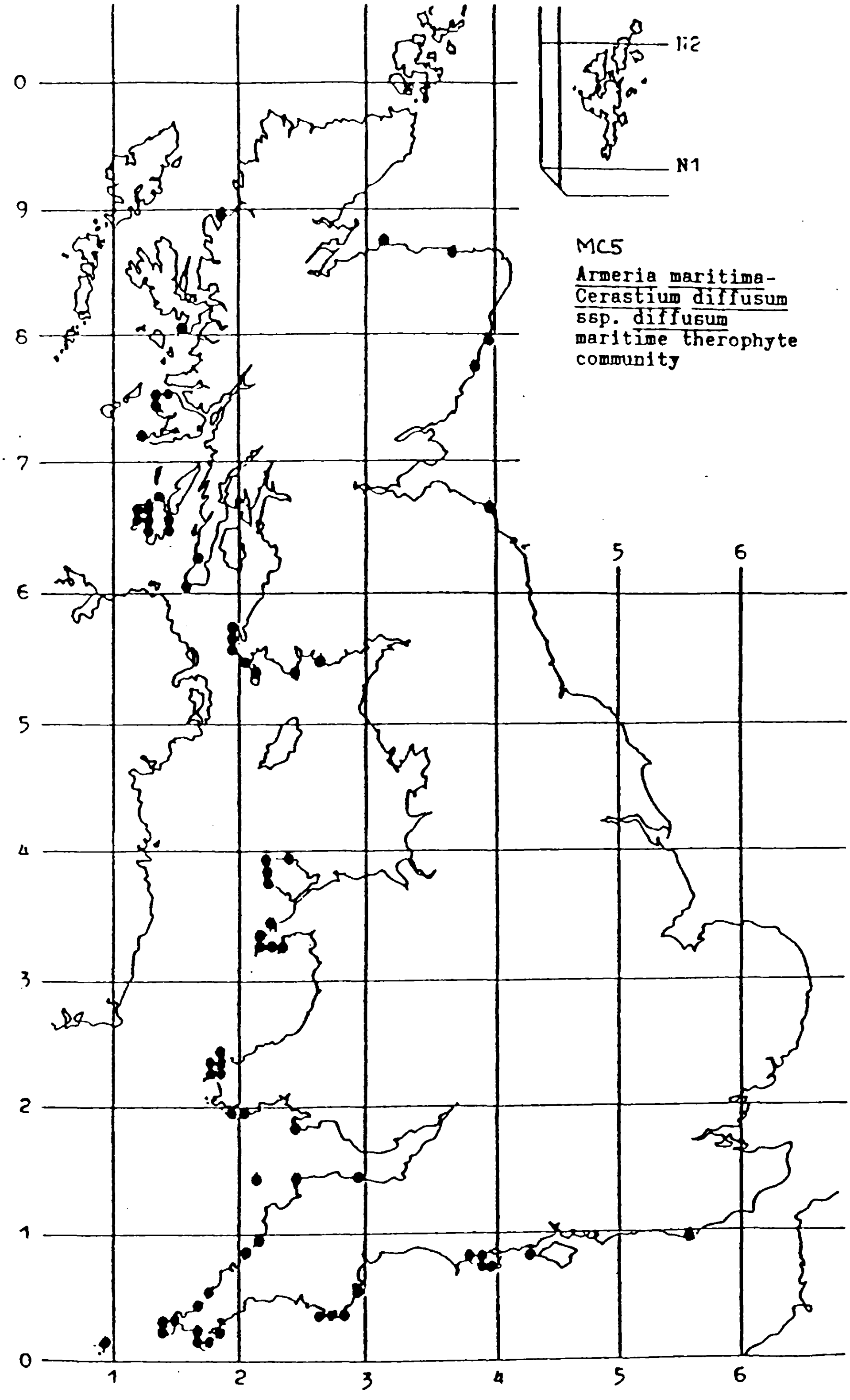
Table 4.17 gives the mean percentage cover ±1 s.e. per study area of the species and other variables listed in Table 4.16. The Domin scale is not

Table 4.16 Plant species (+ 5 other cover types '*') with a frequency of >10% in Welsh study areas (including Stackpole 'W5' and Cornwall), ranked in order of Welsh regional frequency

		No. times present						
Scientific name	Common name	W1	W2	W3	W4	W5	Region	Cornwall
*	Exposed substrate	15	9	12	10	6	52	14
Festuca rubra	Red fescue	8	8	10	7	3	36	8
Holcus lanatus	Yorkshire fog	14	6	5	7	4	36	8
Plantago lanceolata	Ribwort plantain	9	5	12	5	5	36	12
Hypochoeris radicata	Cat's-ear	9	6	6	9	5	35	7
Aira praecox	Early hair-grass	15	5	8	6	0	34	7
Lotus corniculatus	Common bird's-foot-trefoil	9	5	10	4	5	33	4
Plantago coronopus	Buck's-horn plantain	8	3	9	7	6	33	12
Armeria maritima	Thrift	8	3	8	8	3	30	13
Dactylis glomerata	Cock's-foot	8	6	9	6	1	30	12
Sedum anglicum	English stonecrop	9	6	7	6	0	28	11
Aira caryophyllea	Silver hair-grass	5	3	9	4	2	23	8
Scilla verna	Spring squill	4	5	5	5	3	22	1
Jasione montana	Sheep's-bit	7	4	5	5	0	21	3
*	Stones	3	2	8	5	3	21	9
Agrostis tenuis	Common bent	9	3	4	1	1	18	0
Plantago maritima	Sea plantain	7	3	3	3	2	17	1
Cerastium diffusum	Sea mouse-ear	2	0	8	6	0	16	1
Festuca ovina	Sheep's-fescue	3	6	2	5	0	16	7
Centaurium erythraea	Common centaury	2	0	6	4	3	15	2
Silene maritima	Sea campion	2	2	6	3	2	15	6
*	Rabbit dung	1	2	7	0	5	15	4
Cerastium holosteoides	Common mouse-ear	6	4	2	2	0	14	0
*	Rock	2	5	1	2	4	14	7
Thymus drucei	Wild thyme	3	1	3	2	4	13	6
Trifolium repens	White colver	6	1	3	1	2	13	2
Anthoxanthum odoratum	Sweet vernal-grass	8	1	3	0	0	12	2
Bromus ferronii	Least soft-brome	0	1	5	6	0	12	6
Leontodon taraxacoides	Lesser hawkbit	1	2	7	1	1	12	0
Calluna vulgaris	Heather	3	5	3	0	0	11	1
Rumex acetosa	Common sorrel	2	3	3	1	2	11	2
Poa annua	Annual meadow-grass	5	1	3	1	0	10	1
Anthyllis vulnerata	Kidney vetch	1	3	2	4	0	10	5
*	Sheep dung	4	2	2	0	2	10	3
Koeleria cristata	Crested hair-grass	1	1	4	3	0	9	2
Sieglingia decumbens	Heath-grass	3	3	3	0	0	9	0
Achillea millefolium	Yarrow	4	0	4	0	0	8	2
Daucus carota	Wild carrot	0	0	2	6	0	8	8
Festuca sp.	Fescue indet.	4	0	1	0	3	8	1
Galium saxatile	Heath bedstraw	3	3	2	0	0	8	0
Senecio jacobaea	Common ragwort	3	2	2	0	1	8	0
Spergularia rupicola	Rock sea-spurrey	4	1	1	2	0	8	3
Bellis perennis	Daisy	4	1	2	0	0	7	0
Lolium perenne	Perennial rye-grass	4	1	2	0	0	7	2
Rumex acetosella ssp.	Sheep's sorrel	4	2	1	0	0	7	0
Sagina procumbens	Procumbent pearlwort	6	1	0	0	0	7	0
Viola riviniana	Common dog-violet	1	2	2	2	0	7	0
Catapodium marinum	Sea fern-grass	0	1	2	3	0	6	0
Erica cinerea	Bell heather	1	3	2	0	0	6	0
Potentilla erecta	Tormentil	1	4	1	0	0	6	0
Agrostis stolonifera	Creeping bent	1	1	0	2	1	5	2
Galium verum	Lady's bedstraw	0	0	3	0	2	5	0
Prunella vulgaris	Selfheal	2	2	0	0	1	5	0
Teucrium scorodonia	Wood sage	4	1	0	0	0	5	0
Vulpia bromoides	Squirreltail fescue	2	0	3	0	0	5	0
No. of samples		17	11	14	10	6	58	15

Figure 4.15

Distribution of the dominant National Vegetation Classification (NVC) type within British Chough range: *Armeria maritima - Cerastium diffusum* ssp. *diffusum* maritime therophyte sub-community (*cf.* Figure 1.2)



N2
N1
0
9
8
7
6
5
4
3
2
1
0
1
2
3
4
5
6
5
6

MC5

Armeria maritima-Cerastium diffusum ssp. diffusum maritime therophyte community

Table 4.17 Mean percentage cover ±1 s.e. in Welsh study areas with [illegible] region aggregate, and Cornwall; Mann-Whitney regional *z* statistic (N.S. except ** $P<0.01$, * $P<0.05$)

	Mean percentage cover in all quadrats												
Cover type	W1	s.e.	W2	s.e.	W3	s.e.	W4	s.e.	Rgn	s.e.	Cnl	s.e.	*z*
Exposed substrate	13.9	4.6	14.3	7.7	17.2	5.1	12.2	4.4	14.1	2.6	23.4	5.4	1.8
Festuca rubra	8.2	3.1	9.3	3.8	22.6	8.2	17.7	7.4	15.5	3.2	18.1	7.6	0.3
Holcus lanatus	3.6	1.1	2.9	1.1	2.3	1.3	1.7	0.4	2.7	0.5	2.0	1.2	1.4
Plantago lanceolata	1.4	0.5	0.9	0.3	3.1	0.6	1.8	0.8	1.9	0.3	4.7	2.1	0.1
Hypochoeris radicata	3.4	2.4	1.2	0.4	0.8	0.3	3.2	0.9	2.1	0.8	0.9	0.3	0.9
Aira praecox	2.2	0.4	1.2	0.7	1.3	0.3	1.2	0.4	1.4	0.2	1.3	0.4	1.8
Lotus corniculatus	1.6	0.6	0.9	0.3	2.3	0.7	0.7	0.3	1.7	0.3	0.4	0.2	1.5
Plantago coronopus	2.1	0.7	0.5	0.3	3.7	1.3	12.2	5.0	4.8	1.3	6.7	1.5	1.5
Armeria maritima	1.4	0.5	1.3	0.8	2.4	0.9	1.5	0.4	1.9	0.4	8.2	3.1	1.4
Dactylis glomerata	1.8	1.0	1.3	0.4	1.4	0.4	6.3	3.2	2.2	0.7	4.3	1.3	1.3
Sedum anglicum	1.9	0.6	1.9	0.7	3.1	1.0	5.0	2.3	2.5	0.6	4.8	2.2	0.9
Aira caryophyllea	0.5	0.2	0.4	0.2	1.6	0.4	1.1	0.5	0.8	0.2	1.1	0.3	0
Scilla verna	0.9	0.5	0.9	0.4	0.9	0.4	0.6	0.2	0.9	0.2	0.1	0.1	0.2
Jasione montana	0.6	0.1	0.6	0.3	0.9	0.4	0.8	0.3	0.7	0.1	0.3	0.2	0.2
*Stones	2.6	2.5	0.4	0.9	3.0	1.4	3.9	2.9	2.7	1.0	3.6	1.6	0.3
Agrostis tenuis	9.4	3.2	6.1	5.2	3.4	3.0	0.2	0.2	4.9	1.7	0	-	-
Plantago maritima	5.3	3.3	4.0	2.2	6.1	5.9	0.9	0.8	4.8	1.9	0.1	0.1	1.0
Cerastium diffusum	0.3	0.2	0	-	1.4	0.4	1.3	0.4	0.7	0.1	0.2	0.2	0.9
Festuca ovina	0.3	0.2	3.7	1.7	0.8	0.6	5.4	2.3	1.9	0.6	12.8	4.5	3.2**
Centaurium erythraea	0.1	0.1	0	-	0.6	0.2	0.5	0.2	0.4	0.1	0.3	0.2	1.2
Silene maritima	1.2	1.1	0.8	0.7	0.8	0.3	0.4	0.2	0.9	0.4	3.3	2.0	0.9
*Rabbit dung	0.1	-	0.2	0.1	1.0	0.3	0	-	0.5	0.2	1.1	0.6	2.1*
Cerastium holosteoides	0.5	0.2	0.5	0.2	0.2	0.2	0.2	0.1	0.3	0.1	0	-	-
*Rock	0.5	1.8	16.3	7.1	0.2	0.2	4.3	4.2	4.9	1.8	4.3	2.2	1.4
Thymus drucei	0.3	0.2	0.1	0.1	1.4	0.8	8.5	8.3	3.7	1.8	3.1	2.0	0.4
Trifolium repens	1.6	1.0	0.2	0.2	0.9	0.6	0.2	0.2	0.8	0.4	1.3	1.2	0.2
Anthoxanthum odoratum	3.5	1.5	0.3	0.3	0.9	0.6	0	-	1.3	0.5	0.3	0.2	0.7
Bromus ferronii	0	-	0.2	0.2	1.7	0.8	3.3	1.7	1.0	0.4	1.3	0.6	1.3
Leontodon taraxacoides	0.1	0.1	0.3	0.2	1.6	0.6	0.1	0.1	0.6	0.2	0	-	-
Calluna vulgaris	1.4	1.1	7.6	4.4	0.4	0.2	0	-	1.9	1.0	0.1	0.1	1.7
Rumex acetosa	0.1	0.1	0.6	0.3	0.3	0.2	0.1	0.1	0.3	0.1	0.2	0.1	0.1
Poa annua	3.9	2.6	1.6	1.6	0.4	0.2	0.1	0.1	1.6	0.9	0.5	0.5	0.6
Anthyllis vulnerata	0.2	0.2	2.6	1.7	0.1	0.1	1.2	0.8	0.8	0.4	2.5	2.0	0.1
*Sheep dung	0.5	0.2	0.4	0.3	0.1	0.1	0	-	0.3	0.1	0.4	0.2	0.4
Koeleria cristata	0.1	0.1	0.3	0.3	0.8	0.6	0.6	0.3	0.4	0.2	0	-	-
Sieglingia decumbens	0.4	0.2	0.5	0.3	0.5	0.3	0	-	0.3	0.1	0	-	-
Achillea millefolium	0.4	0.2	0	-	0.7	0.3	0	-	0.3	0.1	0.1	0.1	1.7
Daucus carota	0	-	0	-	0.1	0.1	1.5	0.8	0.3	0.2	1.1	0.3	1.3
Festuca sp.	6.1	3.4	0	-	0.6	0.6	0	-	5.8	2.5	5.5	5.5	1.2
Galium saxatile	0.2	0.1	0.5	0.3	0.1	0.1	0	-	0.2	0.1	0	-	-
Senecio jacobaea	0.2	0.1	0.5	0.4	0.1	0.1	0	-	0.2	0.1	0	-	-
Spergularia rupicola	1.1	0.6	0.7	0.7	0.1	0.1	0.5	0.3	0.6	0.2	0.3	0.2	1.5
Bellis perennis	0.4	0.2	0.2	0.2	0.4	0.3	0	-	0.2	0.1	0	-	-
Lolium perenne	5.0	3.5	0.7	0.7	0.7	0.6	0	-	1.8	1.1	2.4	1.6	1.2
Rumex acetosella ssp.	0.4	0.2	0.2	0.1	0.1	0.1	0	-	0.2	0.1	0	-	-
Sagina procumbens	0.5	0.2	0.1	0.1	0	-	0	-	0.2	0.1	0	-	-
Viola riviniana	0.6	0.1	0.2	0.1	0.1	0.1	0.3	0.2	0.1	0.1	0	-	-
Catapodium marinum	0	-	0.1	0.1	0.4	0.2	0.8	0.4	0.2	0.1	0	-	-
Erica cinerea	0.1	0.1	2.2	1.1	1.1	0.8	0	-	0.7	0.3	0	-	-
Potentilla erecta	0.1	0.1	0.6	0.3	0.1	0.1	0	-	0.2	0.1	0	-	-
Agrostis stolonifera	0.1	0.1	0.2	0.2	0	-	0.5	0.3	0.3	0.2	2.4	1.6	2.0*
Galium verum	0	-	0	-	0.7	1.3	0	-	0.4	0.3	0	-	-
Prunella vulgaris	0.2	0.2	0.2	0.1	0	-	0	-	0.1	0.1	0	-	-
Teucrium scorodonia	0.2	0.1	0.1	0.1	0	-	0	-	0.1	-	0	-	-
Vulpia bromoides	0.1	0.1	0	-	1.0	0.6	0	-	0.3	0.2	0	-	-

a linear scale, and the percentage cover given represents a mean around which there might be 10-20% fluctuation depending on season and weather conditions etc. During this survey, drought conditions had applied for several weeks. Table 4.18 provides physiographical information on the Welsh quadrat sites. Figure 4.16 represents the aspect of each, and as can be seen no pattern emerged; in fact, the two majority aspects were diametrically opposed: SE (12) and NW (11).

Table 4.18 Physiography of key feeding site quadrats in which vegetation was recorded

Variable	Measurement	$\bar{x}$	±1s.e.	N
Altitude (a.s.l)	10 - 180m	66m	5.9m	58
Slope	0 - 80°	20°	2.8°	57
Soil-depth	.5 - >80mm	18mm	2.2mm	58
Stand area	1 - 2000m^2	284m^2	63.3m^2	45

A regional significance test (Mann-Whitney) was carried out on the mean percentage cover of the components, despite the different criteria necessary for selection of quadrats (4.4.2). Only 3 cover-types showed significant difference between the regions: *Festuca ovina*, *Agrostis stolonifera* and rabbit dung (Table 4.17); identification problems, due to the drought conditions, concerning the fescue grasses, could possible partly explain the very highly significant difference found in this case.

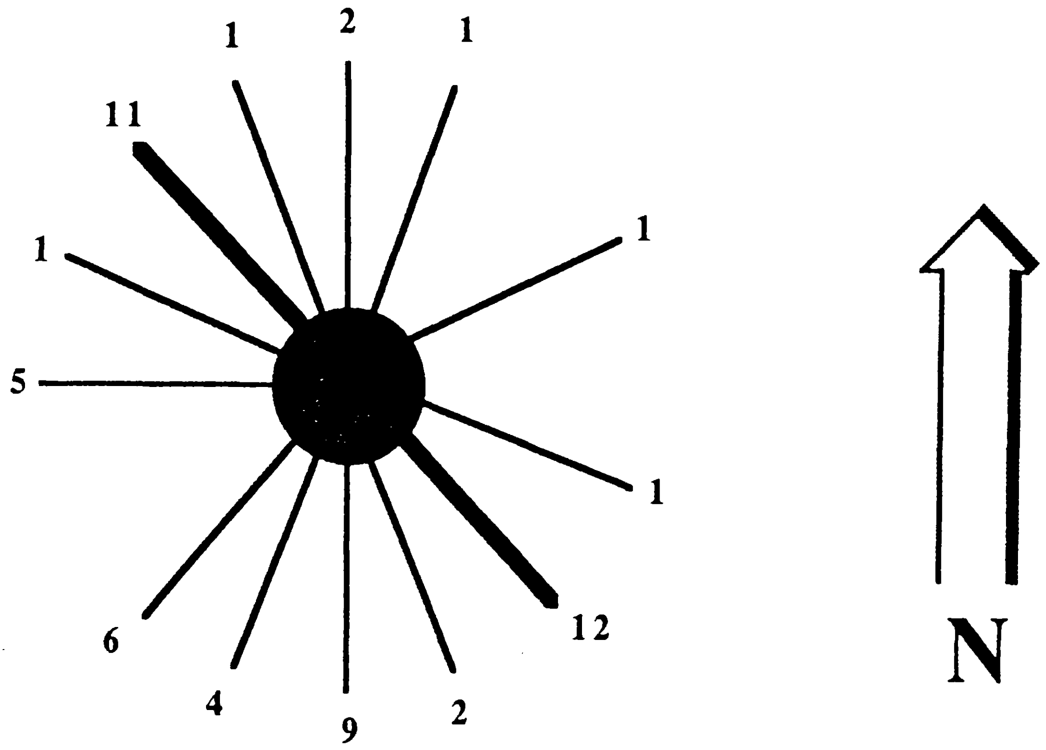


Figure 4.16

Frequency of aspects of sampled key feeding sites surveyed for their botany (N=56, 2 sites were on level ground, *i.e.* no aspect)

4.4.4 DISCUSSION

The extent of the vegetation stands which supported the surveyed sites were not normally distributed (Table 4.18), thus confirming the observation already made that Choughs exploit a wide range of habitat configurations: from small pockets to large zones and fields. The deciding factor is quality not integral size. Effects of altitude are expected to be overshadowed by those of maritime influence (Malloch 1972). This is in accord with NVC descriptions: MC5, in particular (*cf.* Table 4.2), is characteristic of excessively-draining, often very shallow soils at all levels on rocky cliffs; it is often ungrazed although the effects of hard grazing and burning will cause it to expand from its shallow-soiled refugia (S.B. Evans pers. comm.). Floristic variation of MC5 can be related to differences in maritime influence and in bedrock and soil type (Rodwell 1982). The depth of soil was overall very shallow (<2cm; Table 4.18). Nearly a quarter of the feeding-sites also included bare rock, which accounted for nearly 5% cover (Table 4.17).

The degree of slope of sampled sites was influenced by considerations of accessibility and safety, and, therefore, no special significance should be attributed to this part of the description in Table 4.18. Choughs are able to feed on vertical and even overhung cliffs (pers. obs.) and certainly had access not been a seriously limiting factor, more cliff sites, representative of MC1 and MC4 (Table 4.3), would have been sampled.

Many of the species listed in Table 4.16 are of constant or frequent occurrence within various sub-communities of MC8 - MC11 (Table 4.2), others are characteristic of pastoral agriculture and indicate its often close proximity. It is possible to conclude that the botanical communities which represent favourable conditions for Choughs in West Wales are: MC1, MC4, MC5, MC8, MC9, MC10, MC11 and U46. More precisely, the *Aira praecox* sub-community of MC5, represents the most favourable of all recognised communities. MC5 is an edge-type in itself which retains an open state (=sparse vegetation and exposed substrate) by abiotic factors and maritime influence as well as extending this into neighbouring communities by virtue of burning, hard-grazing and other effects of human agency. The over-riding impression gained from this survey was a concentration on ecotones and often difficult to categorise boundaries and peripheral niches and crevices (see frontispiece). *Aira praecox* was found growing in nearly 60% of the 58 quadrats surveyed, but represented a mean cover of less than 2% (Table 4.17), which confirms its status as an indicator species for the purposes of Chough biology. The main cover-types within this survey were *Festuca rubra* and exposed substrate; no other exceeded 5%.

4.5 HISTORICAL HABITAT ASSESSMENT

4.5.1 METHODS

The rationale behind this part of the study was introduced in Section 2.4. Ninety nine coastal 1km^2 from the arrays shown in Figures 2.2 - 2.5 and surveyed during the present-day habitat assessment (Section 2.2 and see Section 4.2) were located on the very large but variably scaled maps (held by the County Record Offices) drawn during the Tithe survey of the mid-C19, and the contemporary land use noted along with appropriate physiological data. The quality of surveying and recording in the 1840s varied considerably from area to area, and this resulted in some maps yielding little or no useful information; occasionally maps were damaged or had portions missing; two maps contained no field-by-field data at all. Where a parish boundary cut through a kilometre square, definitions of obviously homogeneous land types would sometimes vary.

As stated in Chapter 2.4, only rudimentary historical habitat information was available compared to that achieved during the current assessments (Sections 4.2 & 4.5). It fell into broad categories such as 'cliffs', 'rough pasture', 'common', 'arable', 'turbary' (communal turf- or peat-cutting ground), 'furze', 'waste', 'homestead' etc. Detailed information, *cf.* Figure 4.8, was not available. To overcome this problem, land-types were reduced to a classification consistent with known usage practices of the day, *e.g.* "furze and pasture" was classified as "rough grazing", as was "commons/moorland". A similar analytical approach as described in Section 4.2 for the background assessment was employed except that TWINSPAN was not involved.

On 10 maps, field data were not given or merely lumped as, for example, "arable and pasture alternately". Nevertheless, it was usually possible to measure the sizes of fields and, therefore, the extent of permanent boundaries (*i.e.* walls), and this explains the differing sample sizes in Table 4.19. The rectangular pixel configuration is more sympathetic to polygons than narrow linear areas, and, therefore, wall/boundary values are over-estimated unless corrected for. Typical Pembrokeshire and Cornish drystone walls are seldom wider than 2m at their base although their surface area is approximately 1.75 times greater; this area, if grazed or otherwise having negligible vegetation, is available to Choughs. Therefore, 1x2m of wall (0.5%/pixel) gives about 3.5sq.m. (0.875%/pixel) of potential habitat. So, although a simple linear measurement will underestimate wall-surface area, uncorrected rasterized data will overestimate it, due to the fact that any pixel (400 sq.m.) showing wall would be read as solid wall, clearly nonsensical (see Figure 4.17). A straight linear 20x2m of wall (=10%/pixel) corrects to *ca*.70 sq.m. of wall-surface area (=17.5%/pixel), but walls are often angled and abutted by other walls. When random samples of pixels containing walls were scaled-up, it was found that the values were exactly doubled giving a corrected mean wall-surface area per pixel of 35% (±s.e. 1.6%, n=10). To give an estimate of wall-surface area, irrespective of whether it is available to Choughs or not, 400 sq.m. of wall-pixel area is converted to the found average 35sq.m. by the equation: WP(400)/11.429 - where WP is the number of wall-pixels; 11.429 is the factor by which 400 must be divided to give 35.

Tithe information is sketchy and has to be interpreted with care (Kain & Prince 1985). Arable land was the most valuable to commissioners, therefore, never under-recorded, although there was often disagreement between surveyors and farmers as to where the distinction lay between pasture and arable. Generally, 'arable' was defined as land ploughed over the previous 3 years or sometimes the previous 7 years (the period in which the act required tithe receipts to be averaged). Convertible husbandry was widely practiced in the C19 and created problems of interpretation which were exploited by both surveyors and farmers to their own advantage. The pastoral component on Tithe apportionments was often combined with meadowland and sometimes arable. The usual sequence of rotation was that seeds lay for 3 to 10 years before being ploughed. After the first year, when leys were mown for hay, they were pastured until deterioration necessitated ploughing, usually 5-8 years (Kain & Holt 1981).

Figure 4.17

Example of rasterized $1km^2$ (SW4237, Zennor, West Penwith), showing tithed agriculture (top): A=arable, P=pasture, K=common land, H=croft, T=turf, F=furze, Z=shoreline, Y=sea; and boundaries (uncorrected) below: B=boundaries, Z=agriculture, Y=sea. See also Figure 4.18

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S W 4237Agriculture
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Maps were digitized (see Section 2.4), and the rasters (rows of pixels) loaded onto the Prime mainframe computer at Paisley College of Technology. Summary statistics were generated for analysis on microcomputer by SPSS/PC+ (SPSS 1986). Nearly 40% of the total area (97km squares) analysed was accounted for by sea, and for the main analyses, this was excluded and the values corrected to give percentage cover of land surveyed.

Use of tithe data to estimate numbers of livestock must be exercised with great caution, although Cornwall provides some of the best available data (Kain & Prince 1985). Unfortunately, Pembrokeshire farmers often refused to co-operate with commissioners, barring their folds and dairies; the estimated data are not considered reliable (*ibid.*). Kain & Holt (1981) examined the reliable data for Cornwall, and these are later related to present stocking levels within the Cornish regional study area (4.6.2).

4.5.2 RESULTS

The proportions of habitat in Wales and Cornwall as recorded from the tithe survey of the 1840's are given in Table 4.19. For 87km^2 sufficient data existed to make some assessment of contemporary land use, and for an additional 10, measurements of boundaries were obtained. Of the 87 maps from which land-use data were obtainable, 38.9% was accounted for by sea, with very little variance between the two regional blocks (38.02% and 39.61%) indicating that no bias existed in the selection or in the degree of oceanicity between the two sample sets.

The largest proportion of agricultural land was down to arable ($\bar{x}$=37.9% over both regions ±1s.e. 3.1%). There was significantly more in Cornwall

Table 4.19 Mean percentage composition ±1 s.e. of 1km coastal squares in West Wales and Cornwall mapped from tithe data (mid-C19) and measured in 20 m^2 pixels (2500=1km sq), corrected for exclusion of sea

Cover-type	% in Wales		% in Cornwall		Mann-Whitney *z* value	*P*<
	Mean	s.e.	Mean	s.e.		
Sea	38.02	5.20	39.61	4.49	-.4322	N.S.
Excluding sea						
Arable	24.91	3.32	48.00	4.45	-3.408	0.001
Pasture	39.12	3.84	11.09	2.71	-5.523	0.001
Undefined/unknown	18.98	3.63	8.02	2.31	-3.415	0.001
Rough grazing	1.67	0.80	11.02	2.85	-3.350	0.001
Homesteads/crofts	2.22	0.60	3.11	1.07	-0.880	N.S.
Furze	3.50	2.00	4.86	2.31	-2.738	0.01
Turbary	0	0	5.55	1.92	-3.850	0.001
Meadow	5.17	1.23	0.03	0.02	-5.767	0.001
'Arable & pasture'	1.35	0.50	2.91	1.33	-1.279	N.S.
Waste	0.29	0.18	1.40	0.52	-3.348	0.001
'Clifflands'[1]	1.66	0.99	2.23	1.89	-1.371	N.S.
Orchard	0	0	0.53	0.34	-2.595	0.01
Rocks	0.18	0.16	0.22	0.12	-0.526	N.S.
Woods/plantations	0.04	0.02	0.01	0.01	-0.817	N.S.
Scrub	0.03	0.03	0	0	-0.198	N.S.
No. 1km sq's mapped	38		49			
Walls (corrected[2])	6.66	0.56	7.15	0.56	-0.505	N.S.
No. 1km sq's mapped	47		50			

[1] possibly unused, agriculturally

[2] for methods, see text (p.102)

(double) than in Wales ($P<0.001$). There was also more turbary, waste, rough grazing ($P<0.001$) and furze ($P<0.01$) in Cornwall. In Wales, the shortfall was made up by significantly more pasture (both regions $\dot{x}$ =23.3% ±1s.e. 2.7%) and meadow ($P<0.001$), both being products of rotational leys. Unfortunately, there was also a far greater amount of indeterminate land ($P<0.001$) in Wales, and were this land use known, it would almost certainly increase some of the other Welsh proportions, including 'turbary', which was, otherwise, unrecorded in Wales. Orchards scored zero in Wales possibly due to other vagaries of classification (see below). There was no significant difference in the extent of walls between the two regions during the mid-C19: a mean wall-pixel value of nearly 20% (±1s.e. 1.1%) over both regions is corrected to *ca*.7% estimated available area, as described above (4.5.1).

The zero score in Wales for orchards is probably explained by their being valued as much for pasture as for fruit produce, and they were frequently therefore included within the pasture acreage (Kain & Holt 1981). Notwithstanding the 11% balance of undefined land in Wales, the data support the statement in Section 3.4.6e that Cornwall until quite recent times was relatively backward in its agriculture with significantly more rough pasture of various kinds, certainly more than was to be found in Wales, where the agriculture was more improved with significantly greater areas of land down to meadow and pasture. 'Cliffs' (the slopes and horizontal tablelands) were utilised to a considerable extent for only about 2% was not apportioned with a more specific description. A similar percentage was accounted for by buildings and gardens.

4.6 CHANGES IN HABITAT OVER TIME

4.6.1 METHODS

Two methods were used to assess the broad changes in habitat, as they might have affected Choughs, over 150 years (1840-1990). One related the results described in the coastal km^2 analyses described in Sections 4.2 and 4.5; the second compared summaries of coastal parishes obtained from the Tithe Commission apportionments with June 1987 Ministry of Agriculture Fisheries & Food (MAFF) parish summaries. Due to discrepancies in methods of data collection (not designed for ecological purposes), inevitable limitations affected these analyses. It was only possible to undertake fairly crude correlation between them, yet it was hoped they might help to reveal some of the changes in land-use over that period of time.

Coastal parishes in Cornwall and Dyfed within the habitat blocks surveyed during the assessment described in Section 4.2, which provided land-use data over both periods (1830-40's & 1987) are listed in Tables 4.20 & 4.21. This amounted to 47 parishes (24 in Wales and 23 in Cornwall). One Welsh parish (Dale) was tithe documented as 121 acres (49ha), the current size is 459ha (MAFF 1987 June census) and has remained unchanged since feudal times (S. Morrell pers. comm.); to prevent confusion, Dale was omitted from individual parish comparisons. For a further 3 parishes in Wales and one in Cornwall, MAFF could not supply 1987 data. Since a regional overview rather than an individual parish position was required, inter-parish boundary changes, whether actual or effective, were ignored. A paired t-test showed there to be no systematic difference between the mid-C19 and 1987 parish areas (Table 4.22). The mean differences per area were: Wales 1.59%, Cornwall 7.24%; and combined: 4.35%. Changes in recording techniques might account for some of the discrepancies.

Table 4.20 Parishes in Wales surveyed for agricultural use in the mid-C19 and 1980s

Parish	TITHE SURVEY		Comments
	Date	Acreage	
Angle	1841	1994	
Rhoscrowther	*ca*.1840	2227	
Roch	*ca*.1840	4300	
Waltonwest	*ca*.1840	1152	
Nolton	*ca*.1840	1475	
St. Elvis	1837	360	no 1987 data
Whitchurch in Dewsland	1838	3200	
Dale	1847	121	*con*. current data
St. Brides	1839	1703	
Brawdy	1842	5173	
Marloes	1842	2268	
St. Ishmael's	1839	3000	
Llanwnda	1843	4330	
Dinas	1841	2000	
Newport	1844	4372	
Neverne	1840	10290	
Fishguard	1839	3442	
Moylgrove	1847	2370	
St. Dogmael's	1838	5900	
Verwig	1838	3000	
Mwnt	1847	1100	no 1987 data
Aberporth	1838	2100	
Blaenporth	1837	3500	no 1987 data
Penbryn	1838	10000	
Llangranog	1840	4034	
Llandysiliogogo	1841	9182	
Llanllwchaearn	1846	2975	

Table 4.21 Parishes in Cornwall surveyed for agricultural use in the mid-C19 and 1980s

	TITHE SURVEY		
Parish	Date	Acreage	
St. Mawgan in Pydar	1842	6078	
Mullion	1843	5595	
Zennor	*ca*.1840	3184	
Rame	1844	1247	no 1987 data
Padstow	1840	3639	
St. Endellion	1842	3641	
St. Buryan	1844	5468	
St. Minver	1838	6300	
St. Teath	1841	4842	
Tintagel	1842	5173	
Marloes	*ca*.1840	3709	
Grade	1841	1946	
St. Keverne	1840	10158	
St. Anthony in Meneage	1840	1500	
St. Merryn	1841	3608	
St. Eval	1841	2673	
St. Just in Penwith	1845	6500	
Sennen	1838	2050	
Morvah	1839	1120	
St. Levan	*ca*.1840	2100	
Madron	1842	6000	
Towednack	1839	2800	
Gunwalloe	1839	1328	
Landewednack	1841	1929	
Magan in Meneage	1838	5210	

Table 4.22 Mean recorded sizes (ha) ±1 s.e. of parishes in Wales and Cornwall in the two periods

Region	C19	s.e.	1987	s.e.	paired *t*-value	
Wales	3934.22	547.80	3811.01	543.88	.53	N.S.
Cornwall	3972.96	459.00	3436.26	437.60	1.96	N.S.
Mean	3953.59	353.36	3623.67	346.47	1.83	N.S.
t-value	-.05 N.S.		.54 N.S.			

Proportions of pasture (representing advantageous year-round habitat) excluding modern improved pasture and arable (representing non- or only seasonally advantageous habitat), within parishes, were compared over time and between regions. Changes in woodland cover (negative habitat) were also measured. For the purposes of this study, all land recorded as having a pastoral function was included. Data were not available from this source on the spread of urbanisation nor on the indirect effects of an increasing human population, both of which are discussed in Chapter 3.

Data from the present day assessment undertaken by field surveys of $1km^2$ described in Sections 2.4 & 4.2.2 were related to the assessment of the same kilometre squares from the tithe surveys of the 1840's (4.5.1).

4.6.2 RESULTS

Tables 4.19 and 4.23 - 4.26 give the proportions of pasture, arable and woodland in the coastal parishes of Wales and Cornwall respectively, and the changes since the 1840s as revealed by past and present agricultural surveys. With regard to arable land, while there was significantly more in Cornwall than in Wales during the mid-C19 (see Table 4.19), by recent times this difference had disappeared (Table 4.23). ~~In Wales there has been no significant change over time within the coastal parishes compared [illegible]~~ In Cornwall, there has been a great reduction in the amount of land down to arable in these coastal parishes ($P<0.001$), reducing to a negligible level the differences between the two regions; the mean proportion in Wales changed less significantly (.31 to .20, $P<0.01$).

The amount of old pasture has been significantly reduced in Wales but not in Cornwall: from there being very much more in Wales during the mid-C19 (Table 4.19), this disparity had largely disappeared by 1987 (Table 4.24). Whereas in Cornwall there had been less than half of the land down to pasture, in Wales the proportion was well over half. The change is due to generally increasing pastoralism in Cornwall. The inclusion of improved pasture within the modern values (Table 4.24) does not significantly affect the inter-region analysis, and with both pasture and arable land there is now no difference between the two regions. In Cornwall, however, more improved pasture in recent times resulted in a very great general increase in grassland since the tithe survey ($P<0.001$, Table 4.24). It has been mentioned already that improved pasture (in this case leys more recent than 6 years old) are not readily used by Choughs, at least in southern Britain. More important were clifflands; these were variously described as 'waste', 'turbary', 'furze', 'rocks' etc. They were

Table 4.23 Mean proportions ±1 s.e. of arable land in coastal parishes in Wales and Cornwall in the two periods

Region	C19	s.e.	1987	s.e.	Wilcoxon matched pairs Z-value	N	*P*
Wales	.31	.03	.20	.03	-2.585	23	<0.01
Cornwall	.52	.06	.19	.02	-3.984	23	<0.001
Mann-Whitney *z* value	-2.658		-.055				
P	<0.01		N.S.				

Table 4.24 Mean proportions ±1 s.e. of different pasture categories in coastal parishes in Wales and Cornwall in the two periods. Modern values are given both excluding and including intensively improved pasture ('1987 + improved')

Region	C19	s.e.	1987	s.e.	1987 + improved	s.e.	Wilcoxon matched pairs Z-value	N	*P*
Wales	.69	.03	.56	.04			-2.859	23	<0.01
					.77	.02	-2.129	23	<0.05
Cornwall	.45	.06	.52	.05			-.791	23	N.S.
					.76	.02	-3.498	23	<0.001
Mann-Whitney *z* value	-2.408		-.912		-.363				
P	<0.05		N.S.		N.S.				

extensively grazed and existed in Cornwall very much more significantly than in Wales (Table 4.25). While the extent of such clifflands will not have altered significantly between the two regions during the intervening years, a general reduction in grazing from the high levels which existed, certainly in Cornwall, will have seriously reduced the amount of available Chough habitat (*e.g.*, see Figure 4.18).

Table 4.25 Total and mean proportions ±1 s.e. of uncultivated clifflands within the coastal parishes of Wales and Cornwall in the mid-C19

Region	Sum (ha.)	$\bar{x}$	s.e.	No. parishes
Wales	7770	338	156	23
Cornwall	25908	1126	241	23
Mann-Whitney *z*-value	-3.690	$P<0.001$		

Coastal Cornwall was slightly more wooded than Wales in the mid-C19, however the proportion of woodland has increased significantly in the Welsh region over the subsequent 150 years, at the same time, a decrease in Cornwall has resulted in a significant difference now between the two regions (Table 4.26).

Kain & Holt (1981) presented the density of livestock per 100 acres for those Cornish parishes with reliable data; this was not possible for Pembrokeshire (4.5.1). The results from the June 1987 MAFF census are here presented as individuals per parish (Table 4.27) and also converted as in Kain & Holt (*ibid.*) to enable comparison, albeit very limited, over time. When assessed in raw form, there was no significant difference

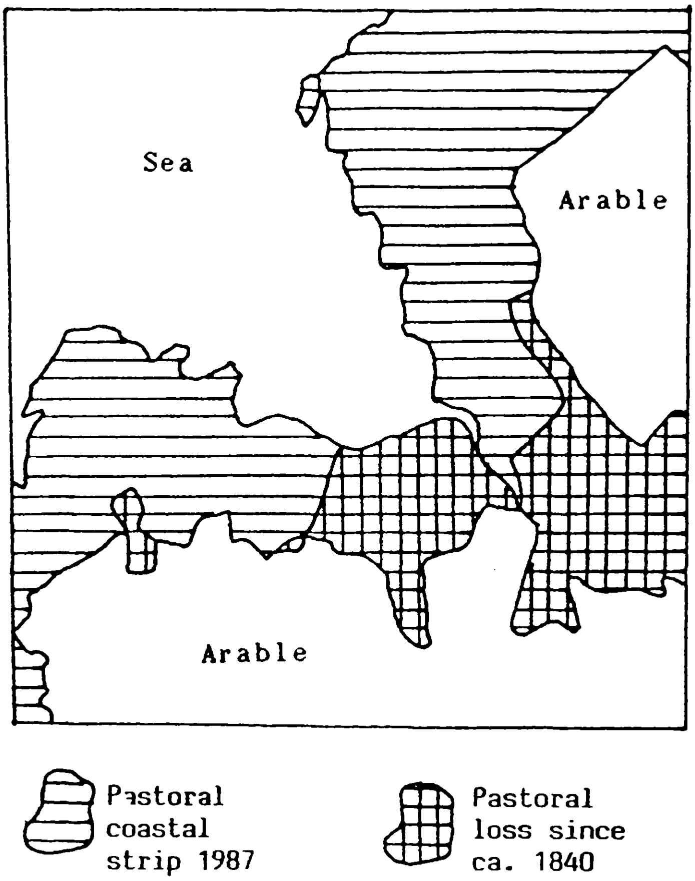

Sea
Arable
Arable
Pastoral coastal strip 1987
Pastoral loss since ca. 1840

Figure 4.18

An example of the decline of coastal pastoral land between 1840 and 1990 within 1km^2 (SW4237, Zennor, West Penwith) of Cornwall; see also Figure 4,17.

NB. Most of what remains is degraded: non-grazed with tall scrub between the regions (although the higher numbers of sheep in Wales approached significance: $P=0.057$), but when converted to density per unit of land irrespective of parish size, significant differences emerged both with sheep and cattle, and it is seen that currently, on the coastlands, Cornwall supports significantly more cattle than Wales ($P<0.05$); Wales supports a very much greater density of sheep than Cornwall ($P<0.01$) (Table 4.27).

Table 4.26 Mean proportions ±1 s.e. of woodland in coastal parishes in Wales and Cornwall in the two periods

Region	C19	s.e.	1987	s.e.	Wilcoxon matched pairs *Z*-value	n	*P*
Wales	.002	0	.017	0	-4.107	23	<0.001
Cornwall	.016	0	.009	0	-2.294	23	<0.05
Mann-Whitney *z*-value	-.290		-2.583				
P	N.S.		<0.01				

In a few parishes in the Cornish study region it was possible to get an insight (but no more) into the measure of changes in stocking levels over the last 150 years (Table 4.28; historical data after Kain & Holt 1981). There was a significant increase over time in the density of cattle ($P<0.05$) but non-significant decrease with respect to sheep.

Table 4.27 Mean numbers of cattle and sheep per parish and per 100 acres in Welsh and Cornish study regions, June 1987 (after MAFF)

	Cattle			Sheep			
Region	$\bar{x}$/parish	$\bar{x}$/100a	s.e.	$\bar{x}$/parish	$\bar{x}$/100a	s.e.	Parish N
Wales	2040	51.4	2.4	4355	90.3	15.8	23
Cornwall	2017	59.8	2.5	1621	40.6	9.8	23
Mann-Whitney *z* value	-0.406	-2.340		-1.901	-2.582		
P	N.S.	<0.05		N.S.	<0.01		

Table 4.28 Mean density of cattle and sheep per 100 acres in Cornish parishes for which reliable data exists (n=7) over the two periods

	Cattle		Sheep	
Period	Density	s.e.	Density	s.e.
1840's	25.7	7.8	25.7	9.0
1987	63.6	3.7	17.6	11.0
Wilcoxon matched-pairs test *Z*-value	-2.366	*P* <0.05	-0.734	N.S.

4.6.3 DISCUSSION

The broad trends in coastal land-use, as they might affect Choughs during the 150 years between the tithe survey and recent MAFF June surveys, are shown in Tables 4.23 - 4.25. From these it can be seen that whereas during the mid-C19 there was significantly more rotational pasture in Wales than Cornwall, this discrepancy had largely disappeared by 1987 (Table 4.24). These results are due to variable increases in pastoralism in both regions, however quality of pasture is more important than quantity, and old pasture was significantly reduced in Wales although not significantly in Cornwall to a point where there was no significance in variability between the regions (*ibid.*). Details of C19 pasture are not known; no doubt the uncultivated so-called wastes, morasses, turbary, furze, rough pasture etc were crucial to Choughs, and it seems likely that due to the importance and extent of tin-mining in Cornwall and the consequent importance of the horse, pony and donkey as draught animals, these uncultivated coastal areas, which existed to a significantly greater extent in Cornwall than Wales (Table 4.25) were also harder grazed there. This would have had the effect of considerably extending naturally favourable botanical communities such as MC8 (4.4). It was clear from an intensive botanical inquiry of prime feeding sites that exposed earth, already identified as crucially important (see Figure 4.8 and Tables 4.5 & 4.9) was the most consistent high-scoring component (Table 4.17); the *Aira praecox* sub-community of MC5, characteristic of edge-types and ecotones, was by far the most important botanical indicator of Chough favourability. It is reasonable to assume that this and herb-rich swards generally would have been commensurately more frequent when stocking rates were much higher and there was no risk of pollution by, for example, invasive *Lolium* rye-grasses and chemical drift. Since ecotones and boundaries between botanical communities contain taxa (flora and fauna) of both adjoining communities plus specialised taxa restricted to the ecotone itself, the population densities of some species are greater here than in the two adjoining regions (Elton 1966), and when this 'edge-effect' incorporates open vegetation or interfaces which Choughs are able to exploit, a more optimal habitat is created. Choughs may therefore select ecotones because they provide unstable, open and accessible conditions, and because prey abundance is increased above that of the surrounding areas.

Analysis of map squares provided better coastal targeting and slightly more detailed data than were available in the parish summaries although the two surveys were complementary. By both methods, the extent of arable land during the mid-C19 was significantly greater in Cornwall than Wales, and the reduction in the former has been very great: from over 50% to less than 20%, compared to a reduction of little more than 10% in Wales (*cf.* Tables 4.19 & 4.22). A reduction in the proportion of arable land has been correlated with increasing Chough success (Williams 1989).

The amount of seeded C19 pasture was significantly greater in Wales than Cornwall (*cf.* Tables 4.19 & 4.23), the significance level, increasing in the field-by-field coastal analysis, suggesting that coastal fringes represent a more extreme example of the typical hinterland agriculture. The relative amounts of 'uncultivated cliffland', shown in Table 4.25, agree with the more detailed breakdown possible from the field survey (Table 4.19): the amounts of rough grazing, furze, turbary and waste were all significantly greater in Cornwall.

Paucity of reliable historical livestock data in the Pembrokeshire study region prevented a meaningful assessment of the changes over time, as was minimally possible for Cornwall. However, the extent of conversion of coastal arable land to intensively improved pasture in both regions (to a very highly significant level in Cornwall (*P*<0.001; *cf.* Tables 4.23 & 4.24) for the use principally of cattle in Cornwall, and presumably sheep in Wales), suggests that the changes in Wales have not been so great as in Cornwall, where agricultural development lagged behind the remainder of mainland Britain (Roberson 1941). A significant increase in the numbers of cattle in Cornwall since the 1840s has not been matched by the sheep population, which, in Wales, is at a level more than double that in Cornwall. Over the period 1875-1950 the numbers of sheep in Britain declined from *ca*.28 millions to less than 21 millions, the decline wholly taking place in England; the sheep population in Wales and Scotland remaining stable or even increasing slightly (Hart 1953). In Cornwall, it was shown (Table 4.27) that sheep numbers had decreased, though not significantly in the few coastal parishes for which reliable data exists. The high numbers of cattle in Cornwall would certainly have helped create good Chough habitat although rough-grazing by cattle possibly needs to be mixed with or followed up by a regime of close-cropping either by sheep or rabbits in order to create the most favourable pastoral conditions for Choughs. The balance in Wales of more sheep/less cattle is probably preferential to that of less sheep/more cattle currently found in Cornwall. On the other hand, the quantity of un-/semi-improved pasture decreased significantly in Wales (*P*<0.01; Table 4.24) within the period under study while the amount available in Cornwall appears to be at a level slightly higher than in the 1840s. It is, however, reasonable to assume that the reduction of grazing pressure since those times, particularly that exerted by horses on the very clifflands of greatest interest (3.4.6e), although unfortunately no hard data exist, has caused a profound reduction on the quality of the pasture and rough grazing.

Therefore, the differences in basic agricultural land-use patterns, which differed greatly in the past between Wales and Cornwall, have now all but disappeared. However, numbers of sheep are at a far lower density in Cornwall than Wales, and previous work by Roberts (1983) in Bardsey to the north, and by Bullock & del-Nevo (1983) in the Isle of Man, has shown that Chough occupancy correlates positively with sheep density. Historically, this could probably be extended to horses as well, and these have certainly decreased dramatically in Cornwall. The effects of a reduced grazing pressure result in a taller vegetation profile, and this was reflected in the Cornish background habitat assessment (4.2.3).

5 FOOD INTAKE

5.1 INTRODUCTION

The slender decurved beak of the Chough suggests fundamental differences between it and the other British corvids (Coombs 1978, Waite 1984, and see Section 1.3.1). Choughs feed largely on epigaeal invertebrates: principally on the larvae of beetles and flies, earwigs, spiders and ants (Goodwin 1986). Cereal grain is recorded as being taken in northern areas (Warnes 1982). Until this study, earthworms have not been regarded as important prey, even though Bullock (1980) reported that 15% of 39 faecal samples from the Lleyn peninsula in North Wales contained such evidence. He recorded none such from nearby Anglesey, nor did Roberts (1982) on neighbouring Bardsey Island, or Warnes (1982) from Islay. Holyoak (1967) suspected that earthworms were taken on the Calf of Man. Ussher & Warren (1900) recorded 'worms' as a food in Ireland but this was somewhat discounted by Bullock *et al.* (1983b).

The aim of this chapter is, primarily by sampling of feeding sites and faecal castings, to investigate the diet of the Chough in West Wales, and to relate these findings to the availability of the prey spectrum by season and in the Welsh and Cornish study areas. It is not here related to habitat availability. Behavioural studies (Chapter 6) demonstrate that Choughs spend virtually all their active time foraging, and areas used for this activity were the subject of the preceding chapter.

5.2 METHODS

5.2.1 PREY SAMPLING METHODS

The term 'prey' is used to describe all food items, whether animate or not. The location of all Chough feeding observations, and, if possible, the actual prey items taken were recorded. If the actual prey was not obvious, either from direct observation or from inspection of prey foci (*e.g.* ants' nests), the area was sampled to give an indication of potential prey present. In Cornwall, the background prey spectrum was sampled in areas which had historically supported Choughs, and which were all potential re-establishment sites (Chapter 7).

The physical and botanical structure of feeding sites were investigated (4.3 & 4.4) in addition to prey sampling. If pursuit of birds was in progress, their positions were marked for later investigation (2.5.3 & 2.5.4). Soil-core extraction was chosen as the primary method of sampling since it could be used both spontaneously and routinely, as determined by Chough behaviour. Although time-consuming, it was considered preferable to the pitfall-trapping used in earlier Chough studies (*e.g.* Warnes 1982) especially when hand-sorting on site. Pitfall-trapping requires pre-selection of sites, fixed equipment and frequent visitation; it is destructive and, in the short term, will alter the local distribution of certain taxa (Terrell-Nield 1986); it is also biased in favour of active ground-moving taxa which are often nocturnal and therefore not Chough food (see below); Southwood (1978) discussed other 'pitfalls' of pitfall-trapping, and Luff (1975) found considerable variation in the efficiency of various traps. However, pitfall-trapping was undertaken during a preliminary study at Rame in Cornwall (Appendix IV), and during an inquiry on Ramsey Island (Appendix V) towards the end of the main study, in which nocturnality and diurnality of the catch assemblages were examined. Suction-trapping was not employed since it samples mainly small invertebrates living on plant stems and leaves, and not larger terrestrial forms, *e.g.* Coleoptera (Galbraith 1986). To sum up, soil-sampling is imitative of Choughs' feeding behaviour, less biased in its selection, and enables instant sampling at recently vacated feeding sites. However, it also under-represents certain taxa, notably carabid ground-beetles which are opportunistically taken by Choughs from the ground surface or from under stones (Coombs 1978); earwigs are possibly also similarly taken.

When access and substrate permitted, soil cores measuring 8x6cm were extracted; otherwise (*e.g.* in rocky ground), an equivalent volume of earth was sampled with a knife or trowel. The depths of cores and their rapid extraction helped to ensure the capture of deep-burrowing earthworms (Galbraith 1986). Inaccessibility of some steep cliff feeding sites will have caused an indeterminate amount of bias.

Spot samples were taken to determine obvious prey (such as ants' nests, as mentioned above, also the foci of diptera larvae, especially in cow dung, and surface items such as cereal grain) at feeding points where these could be determined precisely. Cereal was the only major inanimate food, and because its collection involves surface-gleaning rather than digging or searching, it requires a different analytical approach. It is a food which requires a minimum of collection-effort in terms of time and energy by the Choughs, which offsets its lower calorific value (Richford 1978). Since the food source lies visible on the surface, it cannot be meaningfully sampled in the same way as subterranean fauna; for this reason, cereal grain is omitted from some of the results. Its true value is examined in Section 5.3.5.

Soil samples were immediately disassembled on a white tray or polythene sheet. All organisms of a size likely to be taken by Choughs (*i.e.* >5mm long (5.3.6)) or present in aggregations (*e.g.* ants) were counted; larvae could often be identified only to family or generic level; a type collection was retained for later or specialist examination. Identification was taken to as high a level as possible within available resources. Earthworms were not generally specified but assigned to one of 3 different size classes: S =small (<40mm), M =medium (40-80mm) or L =large (>80mm) (after Feare *et al.* 1974, Waite 1984) [NB. sizes are of animal in relaxed state]; based on a sample of 25 from each class, the energy content of each was S =0.76J, M =1.75J, and L =4.06J (after Waite 1984; *cf.* Table 5.6). The commonest species of earthworm found were *Lumbricus rubellus*, *Eisenia foetida* and *Allobophora chlorotica*; the former two occur in regions of high organic matter, whereas the latter prefers areas where the organic matter has been more broken down (P. Elliott, pers. comm.).

Where precise feeding sites could be determined, sometimes corroborated by definitive evidence of actual prey, these methods ensured that one of the main objectives of the study (the actual components of Chough diet) was adequately covered. At such sites, the method also allowed the frequencies of potential prey to be compared between the different study areas.

At less precisely determined feeding sites, nonetheless determined to exact areas of usage, a transect of 3-5 samples was taken at 1m intervals across the area (Figures 2.15 & 2.16). In order to establish whether Choughs were selecting for localised prey richness (patchiness) or for other reasons, sampling also took place in adjacent habitats which though physiographically suitable for Choughs were unused at the time. Whittaker (1947) noted that Choughs concentrated on certain patches of moorland while avoiding apparently similar patches nearby. The sampling protocol was also intended to provide general background information on prey availability. A second primary objective of the study was the investigation into the availability of potential prey in Cornwall, based on an understanding of prey selection by Choughs in Wales. For this reason, it was necessary to employ a method which could be replicated in areas where Choughs were not currently found (*i.e.* Cornwall), and thus provide a basis for their comparison and a means by which Cornwall and the regions sampled therein could be assessed. Some subjectivity inevitably had to be employed in the selection of equivalent Cornish areas, and this was based on empirical knowledge gained from Chough usage in Wales. The Cornish sampling always took place immediately after Welsh fieldwork to avoid seasonal effects.

Prey abundance and diversity were seen as key elements both to understanding Chough feeding ecology in the different regions of West Wales, and to the assessment of Cornwall as potential Chough habitat. There are two main components of diversity: (i) number of species, and (ii) the spread of individuals (Putman & Wratten 1984; and see Section 5.3.2). An index to estimate availability was constructed to respond to frequency and spread of captures across the study area and region:

$$AI = \frac{(I_a + (S^a - 1)) + (I_b + (S^b - 1)) \ldots}{N}$$

where AI = the Availability Index, I_a = the frequency or total number of individuals per taxon recovered from S^a = the number of +ve samples in the site A ('b' = site B *et seq.*), and N = total number of samples (-ve and +ve) per site or region. A simplified example for a given number of samples, N, is 4 individuals of Taxon *F* from 2 samples would produce 5/N (*i.e.* 4+(2-1)/N), as would also 3 individuals of Species *G* from 3 samples (3+(3-1)/N); thus compensating for the wider occurrence of Species *G*.

The same formula was used both in Chough feeding areas and nearby unused areas in order that they might be compared. The samples in unused areas were arbitrarily selected, as shown in Figure 2.16. The extensive nature of the study did not permit random habitat sampling, and it was, moreover, considered not germaine to the specific objectives: the central question being 'What do Choughs do?' rather than 'What do they not do?'! Given an infinite complexity of habitats and habitat mosaics, the research in Cornwall had to be based on the results from Wales.

5.2.2 FAECAL SAMPLING METHODS

Faecal samples were collected during the course of bird observation. Collection was usually restricted to fresh samples obtained immediately after the birds' departure from a feeding site. Occasionally, these were supplemented with older material, such as in the Rame study (Appendix IV), or to achieve more information on prey selection, where the actual time of defaecation and, therefore, by estimation, of ingestion, was not required. Extra faeces originated from without the main study areas, and some pellets were collected in Cornwall but no accessible roost site was found in Wales, and therefore no pellets were available from Welsh birds.

Faecal samples were usually examined within 24 hours; when this was not possible during the field trip, they were dried and stored for later examination. The collected samples were teased apart in water with the aid of dissecting needles in a glass petri dish beneath a binocular microscope. A magnification of x6.25, illuminated by incident light, was usually found to be sufficient for recording the larger fragments of chitin and other durable prey remains; but this had to be increased to x12.5 - 25.0, with transmitted light, in order to locate earthworm chaetae and, occasionally, the spiracle processes of dipteran larvae. The fragments were sorted, dried on filter paper, and stored in sealed polythene bags. An experiment was tried in which remains from individual faecal residues were 'laminated' between strips of transparent adhesive tape, but it was found that, whilst this was a convenient method of storage, it often proved difficult to examine the microsculpture, scale pattern and form of arthropod fragments, resulting in additional problems of identification.

Since the Choughs foraged over several different habitats in each of the 3 Welsh study areas (Figure 2.1) as well as in Cornwall, this made the study of a comprehensive reference collection of potential prey impossible, particularly in view of the over-riding ornithological nature of the main project. Identification has therefore relied upon direct comparison of the fragments with the extensive entomological collections housed in the University of Sheffield and Doncaster Museum, with the expert help of Dr Paul Buckland. Thus, legs could be identified only to family level amongst most of the Coleoptera, whilst thoraces, elytra and occasionally heads might be taken to the generic or species level. For some groups, *e.g.* the Lepidoptera, insufficient data are available to facilitate identification based upon larval head capsules, and no attempt was made to speciate lumbricid or dipterous processes. Lists of species are not essential and may even be misleading when birds concentrate on a few different dominant items at different times of the year (Feare 1984), as appears to often be the case with Choughs.

In December 1988, a captive Chough was used to investigate food selection, throughput of earthworm chaetae, and calorific intake (Appendix X, and see Section 5.3.7). The results are only of limited application due to the difficulties involved in comparing captive diets with those of wild birds (where digestion of many of the prey leave no recognisable trace in the faeces or pellets), the constraints of environmental and dietary conditioning, and the increased energy costs imposed on wild birds by the need to hunt (see Chapter 6). However, such experiments might be useful if only as a basis for such comparisons and the trial of methodologies.

5.3 RESULTS

5.3.1 PREY SAMPLING AND SELECTION

A total of 1166 soil samples was taken over the course of the study in the main study areas: 658 in Wales and 508 in Cornwall (5.3.4). The discrepancy is partly explained by 138 determinations of actual prey in Wales which were not possible in the main Cornish study, although 56 such samples were collected during the preliminary Rame study (Appendix IV). The origin of samples within the main study areas is given in Table 5.1.

Recorded taxa from Wales are given in Table 5.2 together with an indication of those also recorded from specific feeding points (which reappear in Table 5.4), the study areas from which recorded, and the *AI* or frequency index. The *AIs* of taxa recorded in similar unused 'control' areas adjacent to feeding sites are given in Table 5.3.

Table 5.1 Distribution of soil samples collected in main study areas. The Cornish areas were selected on the basis of empirical Welsh data (see text)

	Number of samples collected in areas			
Study area	Used	Adjacent unused	Feeding	Total
W1:Mwnt-Cemaes	191	44	42	277
W2:Strumble	53	15	25	93
W3:Newgale-Solva	96	6	31	133
W4:Marloes	101	14	40	155
WALES	441	79	138	658
	Equivalent areas			
C1:Pentire-Cant	147	40		187
C2:West Penwith	111	12		123
C3:Lizard	126	72		198
CORNWALL	384	124		508
WALES & CORNWALL	825	203	138	1166

The most frequent potential prey recorded from feeding areas (with an *AI* >.1), which were also present at actual feeding points (Table 5.4), are ranked in Table 5.5. Also given is the respective *AI* from nearby control sites, and the differences. There is a highly significant positive correlation (r_s 0.900, $P=0.01$) showing that Choughs are selecting generally rich invertebrate areas (Figure 5.1). Of these more numerous taxa, only the lumbricids were recorded as more plentiful away from feeding areas. Of the minor taxa, earwigs (Dermaptera) were slightly more numerous in the unused areas (*cf.* Tables 5.2 and 5.3) (see Section 5.4). Earthworms present by far the greatest discrepancy between feeding and control areas; the remaining 5 major invertebrate classes all show increased abundance in feeding areas.

Table 5.2 Taxa, source and index of availability of potential prey recovered from Chough-used areas in Wales. 'I' = no. of individuals (+ = minimum count) recovered from 'S' (no. +ve samples); 'AI' = availability index; 'P' = recorded as possible prey from specific feeding points, 'Y' = yes, 'N' = no (see Table 5.4)

	Availability in study areas																Region
	W1				W2				W3				W4				Region
Taxon	I	S	AI	P	I	S	AI	P	I	S	AI	P	I	S	AI	P	AI
OLIGOCHAETA																	
'Small' lumbricidae	55+	31	.445	Y	3	3	.094	Y	7	6	.125	Y	20	11	.297	N	.299
'Medium' lumbricidae	19	13	.162	Y	12+	5	.302	Y	12	10	.219	Y	10	9	.178	Y	.195
Enchytraeids	13+	7	.099	N	2	1	.038	N	12+	4	.156	N	4	4	.069	Y	.093
'Large' lumbricidae	3	3	.026	N	0	0	0	N	0	0	0	N	0	0	0	N	.011
All OLIGOCHAETA	**88+**	**44**	**.670**	**Y**	**17+**	**8**	**.415**	**Y**	**31+**	**14**	**.438**	**Y**	**34**	**21**	**.515**	**Y**	**.553**
ARACHNIDA																	
Indet. spiders	3+	1	.016	N	4+	2	.094	N	14+	7	.208	N	5	5	.089	Y	.084
Opiliones (harvestmen)	0	0	0	Y	0	0	0	N	15+	5	.198	N	0	0	0	N	.043
Indet. mites	4	2	.026	N	0	0	0	N	0	0	0	N	0	0	0	N	.011
Lycosidae	1	1	0	N	0	0	0	N	1	1	.010	N	0	0	0	N	0
All ARACHNIDA	**6**	**4**	**.047**	**Y**	**4+**	**2**	**.094**	**N**	**30**	**13**	**.417**	**N**	**5**	**5**	**.089**	**Y**	**.138**
CRUSTACEA																	
indet. woodlice	4	3	.031	Y	2	2	.057	Y	1	1	.010	Y	10+	5	.139	Y	.054
Armadillidium sp.	4	1	.021	Y	2	1	.038	N	3	2	.042	N	3+	1	.030	Y	.029
Porcellio scaber	6+	2	.037	N	7	1	.113	N	0	0	0	N	2	1	.020	N	.036
Metoponorthus sp.	11+	5	.079	N	0	0	0	N	0	0	0	N	1	1	.001	N	.036
Philoscia muscorum	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
All CRUSTACEA	**26+**	**12**	**.173**	**Y**	**11**	**4**	**.264**	**Y**	**4**	**3**	**.063**	**Y**	**16+**	**8**	**.199**	**Y**	**.159**
DIPLOPODA																	
Indet. millipedes	0	0	0	N	1	1	.019	N	8	5	.125	Y	4	4	.069	Y	.045

Table 5.2 (continued)

CHILOPODA																
Indet. centipedes	4	3	.031	Y	3+	1	.057	N	2	2	.031	Y	5	5	.089	Y	.048
Pachymarium sp.	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
All CHILOPODA	5	4	.037	Y	3+	1	.057	N	2	2	.031	Y	5	5	.089	Y	.050
DIPLURA																	
Indet. Collembola	0	0	0	N	0	0	0	N	0	0	0	N	2	1	.020	N	0
DERMAPTERA																	
Forficula **sp.**	8+	3	.052	N	2	1	.038	N	2	1	.021	N	0	0	0	N	.032
ORTHOPTERA																	
Indet. grasshoppers	3+	1	.016	N	0	0	0	N	9+	3	.115	Y	15+	5	.188	N	.075
HEMIPTERA																	
Indet. Hermiptera	0	0	0	N	0	0	0	N	0	0	0	N	1	1	.001	N	0
LEPIDOPTERA																	
Indet. Noctuidae	1	1	0	N	0	0	0	N	1	1	.010	N	1	1	.001	N	.001
DIPTERA																	
CYCLORRHAPHA																	
Indet.	5+	2	.031	N	0	0	0	N	0	0	0	N	0	0	0	N	.014
Muscidae	3+	1	.016	Y	0	0	0	N	0	0	0	N	0	0	0	N	.001
Sphaeroceridae	3+	1	.016	Y	0	0	0	N	0	0	0	N	0	0	0	N	.001
Chloropidae	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
All CYCLORRHAPHA	12+	5	.068	Y	0	0	0	N	0	0	0	N	0	0	0	N	.029
NEMATOCERA																	
Tipulidae	38+	22	.309	Y	12+	6	.321	Y	24+	13	.375	Y	26+	12	.386	Y	.338
Bibionidae	3	2	.021	Y	0	0	0	N	3+	1	.031	N	9+	2	.099	N	.039
Chironomidae	0	0	0	N	0	0	0	N	0	0	0	N	1	1	.001	N	0
Sciaridae	0	0	0	N	1	1	.019	N	0	0	0	N	0	0	0	N	0
All NEMATOCERA	41+	24	.330	Y	13+	7	.340	Y	27+	14	.406	Y	36+	14	.475	Y	.381

Table 5.2 DIPTERA (continued)

BRACHYCERA																
Bombyliidae	4	2	.026	N	0	0	0	N	0	0	0	N	0	0	0	Y	.011
Scenopinidae	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
Empididae	1	1	0	Y	0	0	0	N	0	0	0	N	0	0	0	N	0
All BRACHYCERA	**6**	**4**	**.037**	**Y**	**0**	**0**	**0**	**N**	**0**	**0**	**0**	**N**	**0**	**0**	**0**	**N**	**.016**
Indet. Diptera	**18+**	**8**	**.131**	**Y**	**3**	**1**	**.057**	**Y**	**2**	**2**	**.031**	**N**	**1**	**1**	**.001**	**Y**	**.073**
All DIPTERA	**77+**	**40**	**.576**	**Y**	**16+**	**8**	**.396**	**Y**	**29+**	**16**	**.438**	**Y**	**37+**	**15**	**.485**	**Y**	**.499**
HYMENOPTERA																	
Lasius alienus	18+	6	.120	Y	10+	2	.208	Y	22+	9	.313	Y	21+	8	.277	Y	.209
Lasius flavus	3+	1	.016	Y	3+	1	.057	Y	15+	5	.198	Y	12+	5	.158	Y	.093
Indet. ants	0	0	0	N	2	2	.057	Y	18+	7	.250	Y	9+	4	.119	Y	.088
Myrmica sulcinodes	0	0	0	N	0	0	0	N	9+	3	.115	N	0	0	0	Y	.025
Indet. Symphyta sawflies	1	1	0	Y	2	2	.057	N	0	0	0	N	1	1	.001	N	.001
Indet *Myrmica*	0	0	0	N	3+	1	.057	Y	0	0	0	N	0	0	0	N	.001
Myrmica rubra	0	0	0	N	3+	1	.057	N	0	0	0	Y	0	0	0	N	.001
Formicularia fusca	3+	1	.016	N	0	0	0	N	0	0	0	N	0	0	0	N	.001
Formicularia cunicularia	0	0	0	N	0	0	0	N	3+	1	.031	N	0	0	0	N	.001
Tetramorium caespitum	0	0	0	N	0	0	0	N	3+	1	.031	N	0	0	0	N	.001
Indet. *Lasius*	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
(*Lasius* spp.	22+	8	.153	Y	15+	3	.321	Y	37+	14	.510	Y	33+	13	.433	Y	.317)
(*Myrmica* spp.	0	0	0	N	6+	2	.132	Y	9+	3	.112	N	0	0	0	Y	.038)
All HYMENOPTERA	**26+**	**10**	**.142**	**Y**	**23+**	**9**	**.528**	**Y**	**70+**	**26**	**.918**	**Y**	**43+**	**18**	**.548**	**Y**	**.463**

Table 5.2 (continued)

COLEOPTERA																
CARABIDAE																
Indet. carabid	9	7	.079	N	4	2	.094	N	0	0	0	N	1	1	.001	N	.048
Harpalus aenus	6+	4	.047	N	0	0	0	N	0	0	0	N	0	0	0	N	.020
Harpalus rufipes	2	2	.016	N	0	0	0	N	0	0	0	Y	0	0	0	N	.001
Amara aena	0	0	0	Y	1	1	.019	N	1	1	.010	N	1	1	.001	N	.001
Nebria sp.	0	0	0	N	2	2	.057	N	0	0	0	N	0	0	0	N	.001
Notiophylus palustris	2	2	.016	N	0	0	0	N	0	0	0	N	0	0	0	N	.001
Pterostichus ?madidus	3+	1	.016	Y	0	0	0	N	0	0	0	N	0	0	0	N	.001
Harpalus latus	0	0	0	N	0	0	0	N	0	0	0	N	1	1	.001	Y	0
Harpalus tenebrosus	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
Ophonus sp.	0	0	0	N	0	0	0	N	2	1	.021	N	0	0	0	N	0
Leistus sp.	0	0	0	N	1	1	.019	N	0	0	0	N	0	0	0	N	0
Carabus violaceus	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
Carabus problematicus	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
Calathus melanocephalus	0	0	0	N	0	0	0	N	1	1	.010	N	0	0	0	N	0
All CARABIDAE	**25+**	**18**	**.183**	**Y**	**8**	**4**	**.189**	**N**	**4**	**3**	**.042**	**Y**	**3**	**3**	**.030**	**Y**	**.118**
SILPHIDAE sp.	**0**	**0**	**0**	**N**	**0**	**0**	**0**	**N**	**1**	**1**	**.010**	**N**	**5**	**1**	**.050**	**N**	**.014**
STAPHYLINIDAE																
Indet. staphylinid	6+	4	.047	Y	3+	1	.057	Y	1	1	.010	N	0	0	0	N	.029
Tachyporus hypnorum	0	0	0	N	0	0	0	N	1	1	.010	N	0	0	0	N	0
Philonthus varius	0	0	0	N	0	0	0	N	1	1	.010	N	0	0	0	N	0
Philonthus splendens	0	0	0	N	0	0	0	N	1	1	.010	N	0	0	0	N	0
All STAPHYLINIDAE	**6+**	**4**	**.047**	**Y**	**3+**	**1**	**.057**	**Y**	**4**	**4**	**.042**	**N**	**0**	**0**	**0**	**N**	**.036**
ELATERIDAE																
Indet. elaterid	6	3	.042	Y	3	1	.057	Y	0	0	0	N	0	0	0	Y	.025
Agriotes sp.	6	6	.058	N	0	0	0	N	0	0	0	N	0	0	0	N	.025
Steniopus sp.	0	0	0	N	1	1	.019	N	0	0	0	N	0	0	0	Y	0
Ctenicerus sp.	0	0	0	N	1	1	.019	N	0	0	0	N	0	0	0	N	0
Athous haemorrhoidalis	0	0	0	N	0	0	0	N	1	1	.010	N	0	0	0	N	0
Indet. *Athous*	1	1	0	N	0	0	0	N	0	0	0	N	0	0	0	N	0
All ELATERIDAE	**13**	**10**	**.105**	**Y**	**5**	**3**	**.094**	**Y**	**1**	**1**	**.010**	**N**	**0**	**0**	**0**	**N**	**.059**
MELOIDAE sp.	**0**	**0**	**0**	**N**	**0**	**0**	**0**	**N**	**3+**	**1**	**.031**	**N**	**0**	**0**	**0**	**N**	**.001**

Table 5.2 COLEOPTERA (continued)

TENEBRIONIDAE																
Cylindronotus laevioctostriatus	5	5	.047	N	3	3	.094	N	0	0	0	N	0	0	0	N	.032
Cylindronotus striatus	3+	1	.016	N	0	0	0	N	0	0	0	N	0	0	0	N	.001
All TENEBRIONIDAE	8+	6	.063	N	3	3	.094	N	0	0	0	N	0	0	0	N	.039
SCARABAEIDAE																	
Indet. scarabid	11+	9	.099	Y	4+	2	.094	Y	2	1	.021	Y	1	1	.001	N	.061
Aphodius sp.	6+	2	.037	Y	0	0	0	N	0	0	0	Y	0	0	0	N	.016
All SCARABAEIDAE	17+	11	.141	Y	4+	2	.094	Y	2	1	.021	Y	1	1	.001	N	.077
Indet. beetles	0	0	0	N	1	1	.019	Y	1	1	.010	N	1	1	.001	N	.001
All COLEOPTERA	69+	49	.518	Y	24+	13	.547	Y	12	10	.125	Y	5	5	.050	Y	.336
GASTROPODA																	
Indet. slug	5+	3	.037	N	0	0	0	N	2	2	.031	N	0	0	0	N	.023
Nemoralis sp.	2	2	.016	N	0	0	0	N	0	0	0	N	0	0	0	N	.001
Indet. snail	0	0	0	N	0	0	0	N	0	0	0	N	1	1	0	N	0
All GASTROPODA	7+	5	.052	N	0	0	0	N	2	2	.031	N	1	1	0	N	.032
Diversity index *D*		19.6				14.5				14.8				12.6			26.6
Total no. samples		191				53				96				101			441

Diversity index after Margalef (1951), see text p.128

Table 5.3 Taxa, source and index of estimated availability of potential invertebrate prey recovered from unused sites adjacent to feeding areas in Wales. 'I' = no. of individuals (+ = minimum count) recovered from 'S' (no. +ve samples); 'A' = availability index

	Availability in study areas												
	W1			W2			W3			W4			Region
Taxon	I	S	AI	I	S	AI	I	S	AI	I	S	AI	AI
OLIGOCHAETA													
'Small' lumbricidae	26	14	.886	0	0	0	0	0	0	0	0	0	.494
'Medium' lumbricidae	17	10	.591	0	0	0	0	0	0	0	0	0	.329
'Large' lumbricidae	5	4	.182	1	1	.067	0	0	0	0	0	0	.114
All LUMRICIDAE	**48**	**28**	**1.659**	1	1	.067	0	0	0	0	0	0	.937
ARACHNIDA													
Lycosidae	0	0	0	0	0	0	0	0	0	2	2	.214	.038
CRUSTACEA													
Metoponorthus sp.	2	2	.068	0	0	0	0	0	0	1	1	.053	.051
Amphipod	0	0	0	0	0	0	0	0	0	2	2	.211	.038
All CRUSTACEA	2	2	.068	0	0	0	0	0	0	3	3	.357	.101
DIPLOPODA													
Indet. millipedes	2	1	.045	0	0	0	0	0	0	0	0	0	.025
CHILOPODA													
Indet. centipedes	0	0	0	0	0	0	0	0	0	2	2	.214	.038
DERMAPTERA													
***Forficula* sp.**	0	0	0	0	0	0	3+	1	.500	0	0	0	.038
DIPTERA													
NEMATOCERA													
Tipulidae	12	8	.432	5	4	.533	0	0	0	0	0	0	.342
Bibionidae	2	1	.045	0	0	0	0	0	0	0	0	0	.025
All NEMATOCERA	14	9	.500	5	4	.533	0	0	0	0	0	0	.367
Indet. Diptera	1	1	.023	0	0	0	0	0	0	0	0	0	.013
All DIPTERA	15	10	.500	5	4	.533	0	0	0	0	0	0	.443

Table 5.3 (continued)

HYMENOPTERA														
Lasius flavus		8+	3	.227	0	0	0	0	0	0	0	0	0	.127
Indet. *Lasius*		7+	1	.159	0	0	0	0	0	0	0	0	0	.089
Lasius mixus		0	0	0	0	0	0	0	0	0	5	2	.429	.076
Indet. Symphyta (sawflies)		0	0	0	0	0	0	1	1	.167	0	0	0	.013
All HYMENOPTERA		**15+**	**4**	**.386**	**0**	**0**	**0**	**1**	**1**	**.167**	**5**	**2**	**.429**	**.304**
COLEOPTERA														
CARABIDAE														
Indet. carabid		1	1	.023	2	1	.133	0	0	0	0	0	0	.038
Amara curta		2	2	.068	0	0	0	0	0	0	0	0	0	.038
Pterostichus madidus		2	2	.068	0	0	0	0	0	0	0	0	0	.038
Harpalus anxius		0	0	0	0	0	0	1	1	.167	0	0	0	.013
Indet. *Harpalus*		1	1	.023	0	0	0	0	0	0	0	0	0	.013
All CARABIDAE		**6**	**6**	**.182**	**2**	**1**	**.133**	**1**	**1**	**.167**	**0**	**0**	**0**	**.139**
STAPHYLINIDAE														
***Philonthus* sp.**		**1**	**1**	**.023**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**.013**
ELATERIDAE														
Agriotes sp.		3	1	.068	0	0	0	0	0	0	0	0	0	.038
Indet. elaterid		1	1	.023	1	1	.067	0	0	0	0	0	0	.025
Ctenicerus aenus		1	1	.023	0	0	0	0	0	0	0	0	0	.013
All ELATERIDAE		**4**	**3**	**.114**	**1**	**1**	**.067**	**0**	**0**	**0**	**0**	**0**	**0**	**.063**
TENEBRIONIDAE														
***Cylindronotus* sp.**		**2**	**2**	**.068**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**.038**
SCARABAEIDAE														
Indet. scarabid		**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**2**	**2**	**.214**	**.038**
Indet. beetles		**1**	**1**	**.023**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**.013**
All COLEOPTERA		**15**	**13**	**.409**	**3**	**2**	**.267**	**1**	**1**	**.167**	**2**	**2**	**.214**	**.316**
GASTROPODA														
Indet. slug		**2**	**2**	**.068**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**.038**
Diversity index	*D*		10.0			3.1			2.9			4.4		13.3
Total no. samples			44			15			6			14		79

Diversity index after Margalef (1951), see text p.128

Table 5.4 Taxa, source and frequency (number of positive samples / total number of samples) of prey recovered from precise feeding sites in Welsh study areas.

	Frequency in				
	Study areas				
Taxon	W1	W2	W3	W4	Region
OLIGOCHAETA					
'Medium' lumbricidae	.071	.042	.065	.100	.072
'Small' lumbricidae	.143	.042	.032	0	.058
Enchytraeidae	0	0	0	.075	.022
All Oligochaeta	.190	.040	.097	.175	.130
ARACHNIDA					
Indet. spiders	0	0	0	.075	.022
Oedothorax fuscus	.024	0	0	0	.001
Thomisidae	.024	0	0	0	.001
Opiliones	.024	0	0	0	.001
All ARACHNIDA	.071	0	0	.075	.043
CRUSTACEA					
Indet. woodlice	.048	.167	.032	.050	.065
Armadillidium sp.	.024	0	0	.025	.014
Amphipoda	0	0	0	.05	.014
All CRUSTACEA	.071	.167	.032	.125	.094
DIPLOPODA					
Indet. millipedes	0	0	.032	.150	.051
CHILOPODA					
Indet. centipedes	.024	0	.032	.025	.022
ORTHOPTERA					
Indet. grasshoppers	0	0	.032	0	.001

Continued ....

Table 5.4 continued

Taxon	W1	W2	W3	W4	Region
DIPTERA					
CYCLORRHAPHA					
Sphaeroceridae	.119	0	0	0	.036
Muscidae	.024	0	0	0	.001
Agromyzidae	.024	0	0	0	.001
All CYCLORRHAPHA	.167	0	0	0	.051
NEMATOCERA					
Tipulidae	.167	.240	.032	.175	.152
Bibionidae	.095	0	0	0	.029
Mycetophilidae	0	.040	0	.025	.014
Ceratopogonidae	0	0	0	.025	.001
All NEMATOCERA	.262	.280	.032	.225	.203
BRACHYCERA					
Empididae	.071	0	0	0	.022
Piophilidae	0	.040	0	0	.001
Bombylidae	0	0	0	.025	.001
All BRACHYCERA	.071	.040	0	.025	.036
Indet. diptera	.048	.240	0	.025	.065
All DIPTERA	.405	.440	.032	.275	.290
HYMENOPTERA					
Lasius alienus	.167	.040	.419	.200	.210
Lasius flavus	.095	.040	.065	.150	.094
Indet. ants	0	.080	.172	.161	.065
Indet. *Lasius*	0	.080	0	0	.014
Myrmica rubra	0	0	.065	0	.014
Indet. *Myrmica*	0	.080	.032	0	.014
Lasius niger	0	0	.032	0	.014
Myrmica sulcinodes	0	0	0	.025	.001
Lasius brunneus	.022	0	0	0	.001
Tapinoma erraticum	.022	0	0	0	.001
Symphyta/sawflies	.022	0	0	0	.001
All HYMENOPTERA	.310	.320	.774	.425	.442

Continued ....

Table 5.4 continued

Taxon	W1	W2	W3	W4	Region
COLEOPTERA					
CARABIDAE					
Amara consularis	0	.040	0	0	.001
Harpalus rufipes	0	0	.032	0	.001
Harpalus latus	0	0	0	.025	.001
Amara aena	.024	0	0	0	.001
Pterostichus sp. (?*madidus*)	.024	0	0	0	.001
Indet. *Amara*	.024	0	0	0	.001
All CARABIDAE	.071	.040	.032	.025	.043
HYDROPHILIDAE					
Sphaeridium lunatum	.024	0	0	0	.001
STAPHYLINIDAE					
Indet. Staphylinidae	.024	.080	0	0	.021
ELATERIDAE					
Indet. Elateridae	.024	.040	0	.050	.029
Steniopus sulphurus	0	0	0	.025	.001
All ELATERIDAE	.024	.040	0	.075	.036
BYRRHIDAE					
Indet. Byrrhidae	.022	0	0	0	.001
TENEBRIONIDAE					
Cylindronotus laevioctostriatus	0	0	0	.050	.021
SCARABAEIDAE					
Indet. Scarabaeidae	.143	.200	.065	0	.094
Aphodius sp.	.024	0	.033	0	.014
All SCARABAEIDAE	.167	.200	.097	0	.116
Indet. beetles	0	.042	0	0	.001
All COLEOPTERA	.310	.280	.097	.150	.210
CEREAL GRAIN	.048	0	.129	.150	.087
Total no. samples	42	25	31	40	138

Figure 5.1

The relationship between the abundance of principal invertebrate prey taxa in feeding areas and their availability in surrounding areas. Data from Tables 5.2 and 5.3.

Spearman rank correlation coefficient:

$r_s = 0.900$, $P = 0.01$, $n=10$

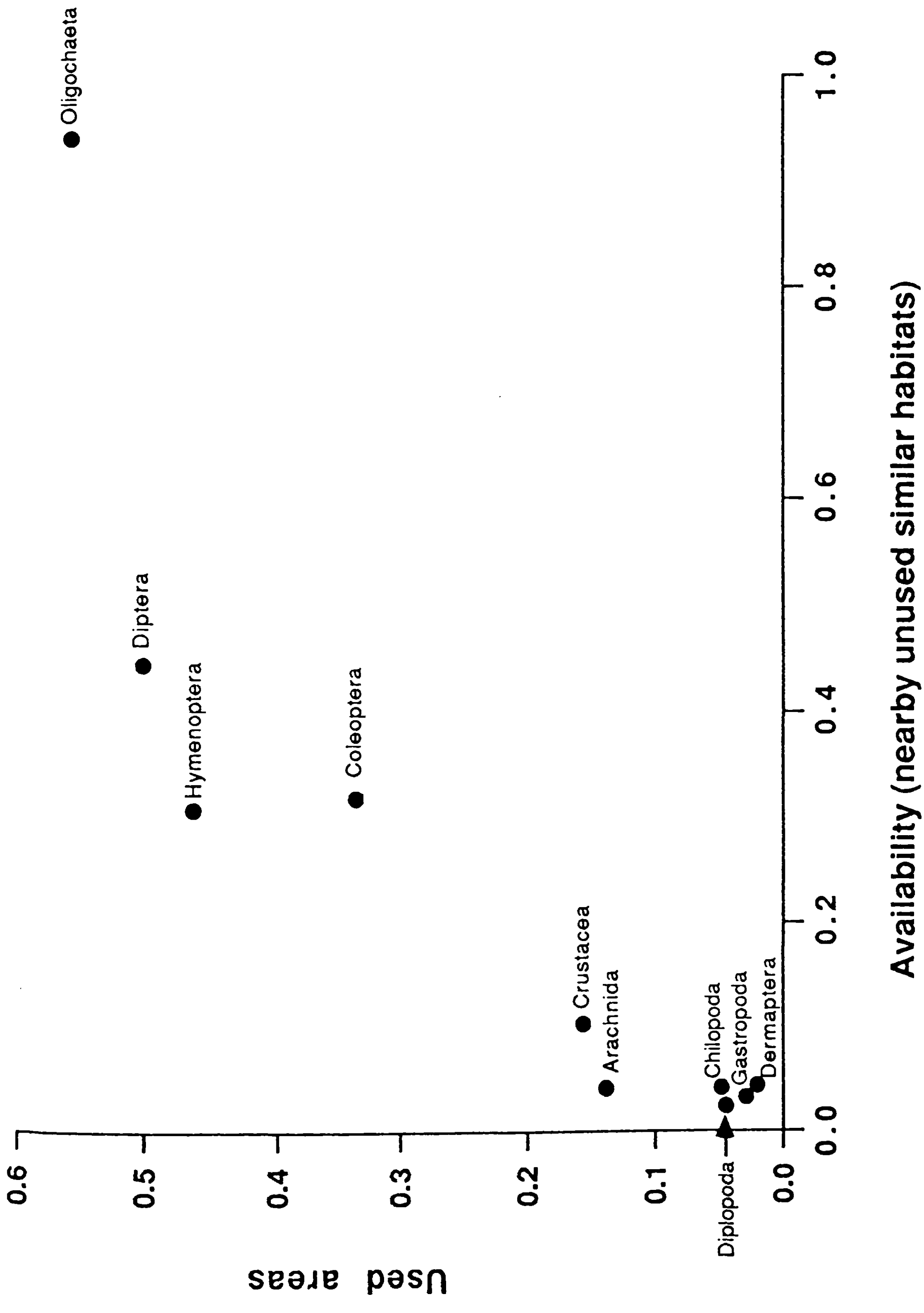

Used areas
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Availability (nearby unused similar habitats)
0.0
0.2
0.4
0.6
0.8
1.0
Oligochaeta
Diptera
Hymenoptera
Coleoptera
Crustacea
Arachnida
Chilopoda
Gastropoda
Dermaptera
Diplopoda

Table 5.5 Summary of Tables 5.2 and 5.3. Principal prey taxa (with regional *AI* >.1) recovered from feeding areas and nearby unused areas (regional r_s 0.946, *P*<0.01, n=6); '+' value signifies greater abundance in feeding areas

	Availability (*AI*) in						
	Feeding sites in Study areas					Unused areas	
Taxon	W1	W2	W3	W4	Region	Region	Regional difference
OLIGOCHAETA	.670	.415	.438	.515	.553	.937	-.384
DIPTERA	.576	.396	.438	.485	.499	.443	+.056
HYMENOPTERA	.162	.491	.938	.564	.463	.304	+.159
COLEOPTERA	.518	.547	.125	.050	.336	.316	+.020
CRUSTACEA	.173	.264	.063	.199	.159	.101	+.058
ARACHNIDA	.047	.094	.417	.089	.138	.038	+.100

Figures 5.2a-b show the abundancies of prey in the feeding areas in the Welsh region and each of the 4 study areas therein. If all invertebrate classes are included in the analysis (*i.e.* including those with *AI*<.1), the highly significant association between feeding and control areas remains (r_s 0.877, n=14, *P*<0.01).

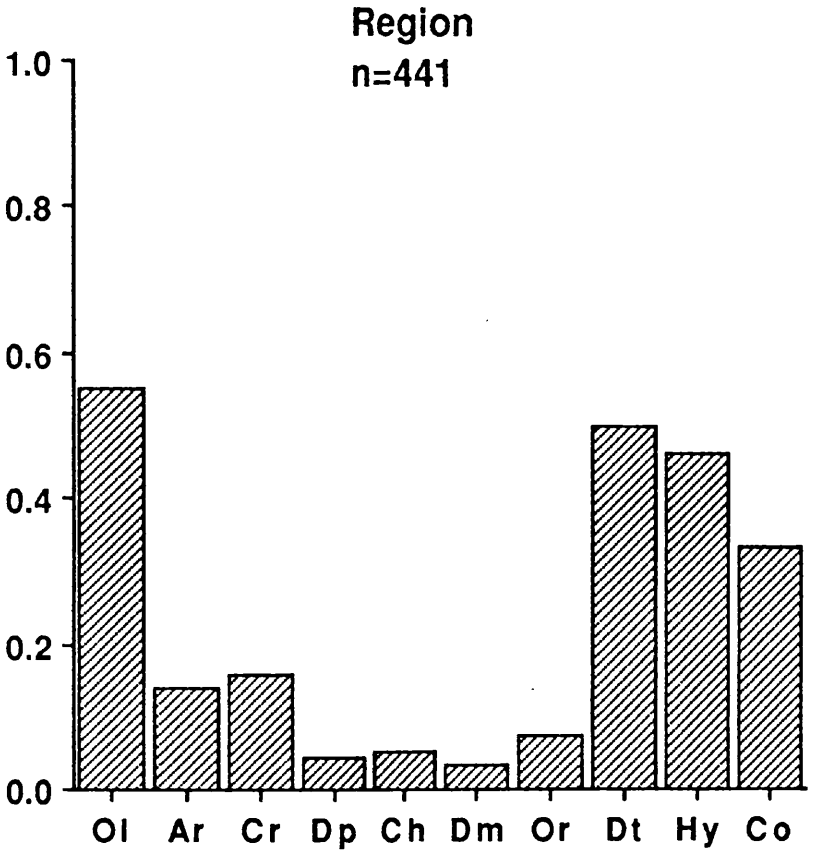
The main prey taxa (*AI* >.1) are Oligochaeta (lumbricid earthworms), Diptera (cranefly and dungfly larvae), Hymenoptera (ants), Coleoptera (Carabidae, Scarabaeidae, Elateridae, Tenebrionidae and Staphylinidae beetles), Crustacea (woodlice) and Arachnida (spiders and harvestmen). The indices of availability respond only to numbers of organisms and not to varying body sizes or calorific values (see Table 5.6, and Appendix X). The extra cost of feeding on small-bodied hymenopterans will be offset to some degree by their occurrence in large aggregations, for example ants of the *Lasius* genus (*AI*=.317), similarly with the smaller

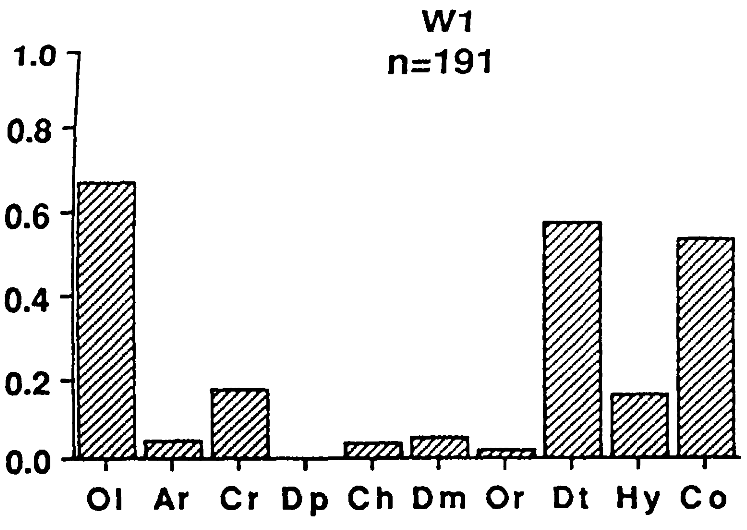
Figure 5.2a-b

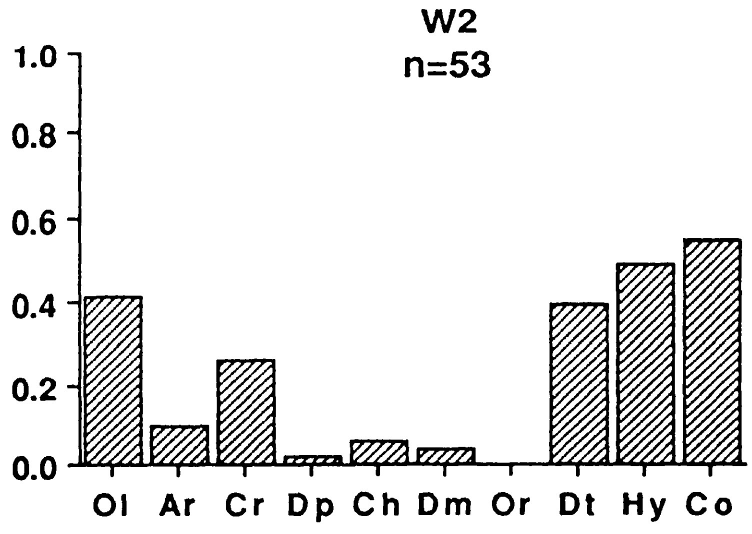
Availablity of principal invertebrate prey taxa (data from Table 5.2) in feeding areas within Welsh region (5.2a) and individual study areas (5.2b)

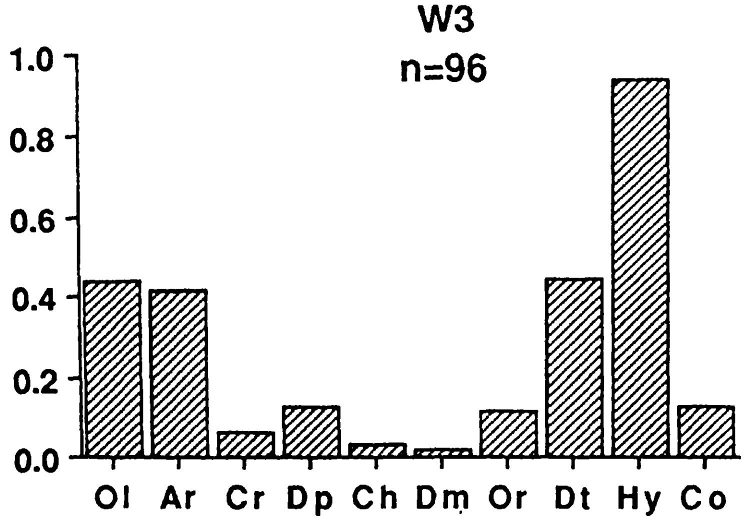
Key:

Ol	Oligochaeta
Ar	Arachnida
Cr	Crustacea
Dp	Diplopoda
Ch	Chilopoda
Dm	Dermaptera
Or	Orthoptera
Dt	Diptera
Hy	Hymenoptera
Co	Coleoptera


Region
n=441
1.0
0.8
0.6
0.4
0.2
0.0
Ol
Ar
Cr
Dp
Ch
Dm
Or
Dt
Hy
Co


W1
n=191
1.0
0.8
0.6
0.4
0.2
0.0
Ol
Ar
Cr
Dp
Ch
Dm
Or
Dt
Hy
Co


W2
n=53
1.0
0.8
0.6
0.4
0.2
0.0
Ol
Ar
Cr
Dp
Ch
Dm
Or
Dt
Hy
Co


W3
n=96
1.0
0.8
0.6
0.4
0.2
0.0
Ol
Ar
Cr
Dp
Ch
Dm
Or
Dt
Hy
Co

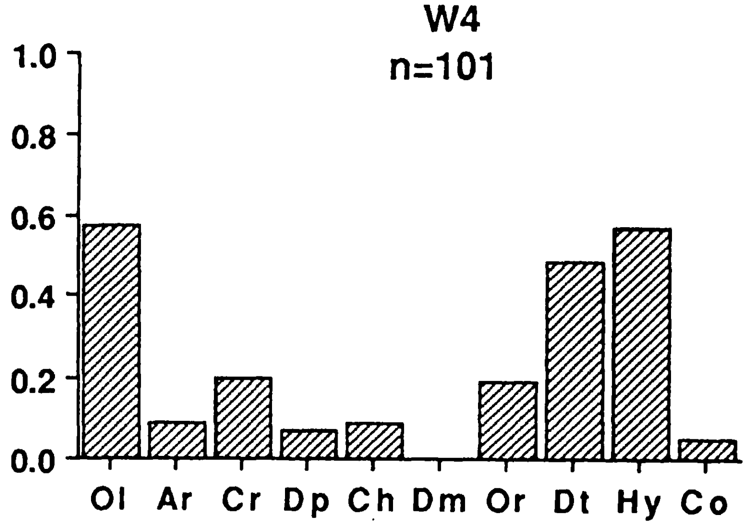
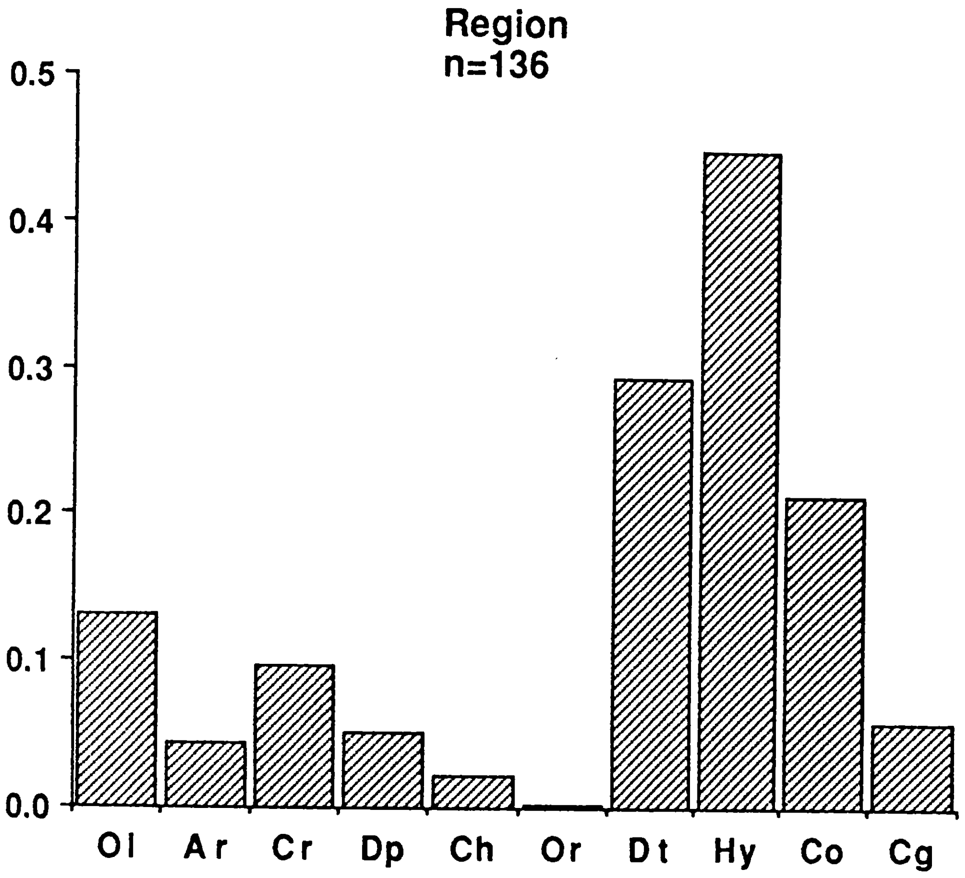

W4
n=101
1.0
0.8
0.6
0.4
0.2
0.0
Ol
Ar
Cr
Dp
Ch
Dm
Or
Dt
Hy
Co

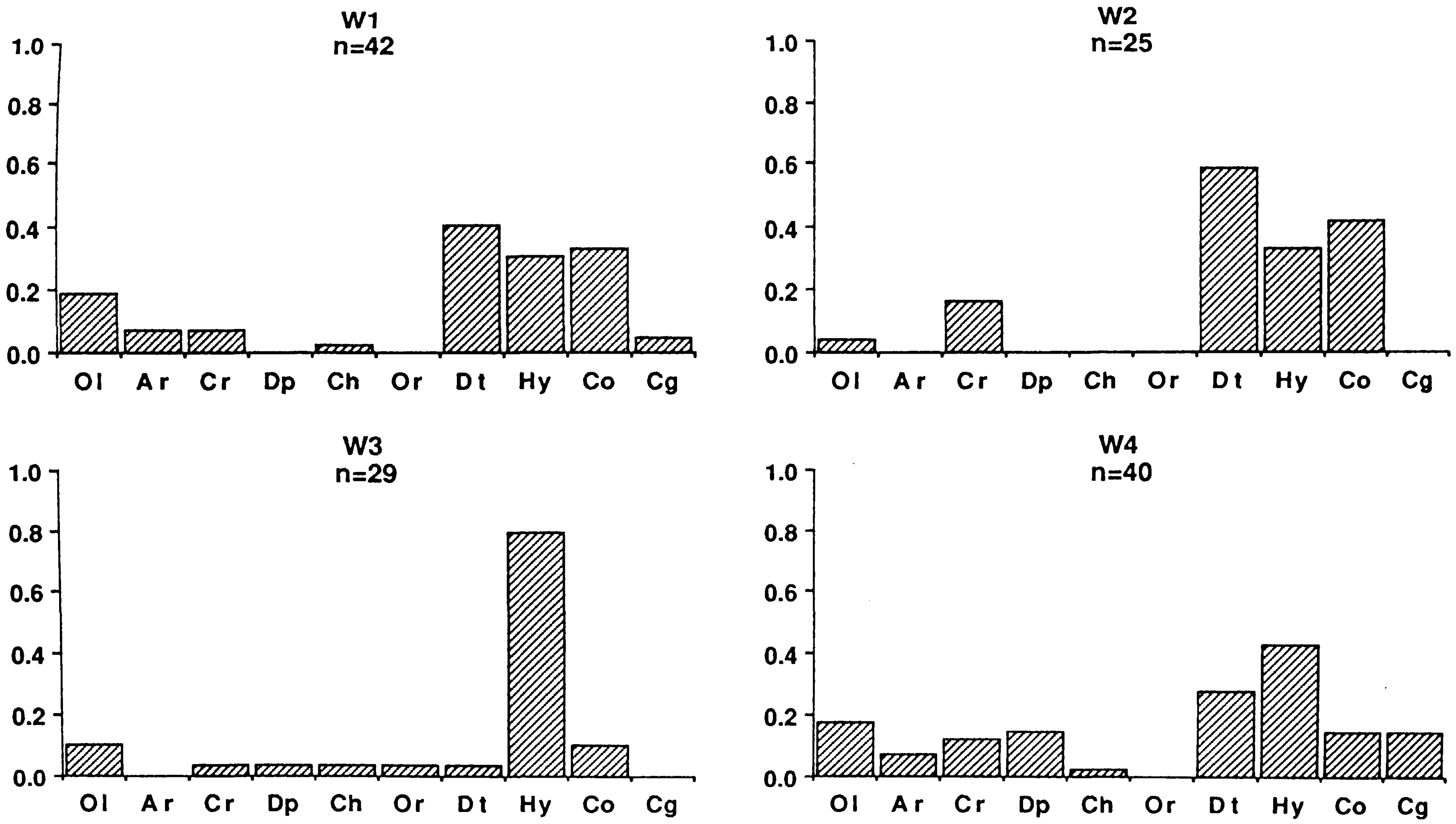
Figure 5.3a-b

Frequency of prey recovered from specific feeding sites (data from Table 5.4) within Welsh region (5.3a) and individual study areas (5.3b)

Key:

Ol	Oligochaeta
Ar	Arachnida
Cr	Crustacea
Dp	Diplopoda
Ch	Chilopoda
Or	Orthoptera
Dt	Diptera
Hy	Hymenoptera
Co	Coleoptera
Cg	Cereal grain


Region
n=136
0.5
0.4
0.3
0.2
0.1
0.0
Ol
Ar
Cr
Dp
Ch
Or
Dt
Hy
Co
Cg


W1
n=42
W2
n=25
W3
n=29
W4
n=40
1.0
0.8
0.6
0.4
0.2
0.0
Ol
Ar
Cr
Dp
Ch
Or
Dt
Hy
Co
Cg

dipterous larvae (*AI*=.499). *Lasius* ants were present in all 4 study feeding areas (*AI*=.153 (Mwnt-Cemaes) to .510 (Newgale-Solva)). *Myrmica* ants were recorded from feeding areas in all but Mwnt-Cemaes but at far lower densities than *Lasius* spp. *L. alienus* (.209) and *L. flavus* (.093) were by far the commonest two prey species. Sawfly (Symphyta) larvae were recorded in 3/4 of the study feeding areas, and form a substantially sized prey item compared to other recorded hymenoptera (Table 5.2).

Cereal grain, as already stated, being inanimate and lying as stubble on the surface of the ground, cannot and should not be sampled or assessed in the same way as live invertebrates, which actively conceal themselves. It has already been shown (Chapter 4) that arable land is used more where it replaces pastoral agriculture, and where a bird breeds influences where it forages (Richford 1978). In Newgale-Solva and Marloes, the most improved, agriculturally, of the study areas (4.3.4), cereal grain was found as frequently at feeding sites as coleoptera, if not more so (Table 5.4); this was not the case at Mwnt-Cemaes and Strumble.

Table 5.6 Approximate energy values of main prey items; A=adult, L=larva (after Torvik & Ludvig 1988, except '*' after McDonald *et al.* 1988)

Taxon	kJ/g $^{-1}$
Lumbricidae	20.0
Arachnida	25.1
Crustacea	15.9
Diplopoda	14.3
Chilopoda	20.9
Dermaptera	26.8
Hermiptera (A/L)	26.8
Lepidoptera (L)	22.5
Diptera (L)	24.2
Hymenoptera (A)	21.3
Coleoptera (A/L)	23.4
Cereal grain	13.0*

From the data presented in Table 5.4 and summarised in Figures 5.3a-b, based on investigations of probable prey at precise feeding points immediately following the birds' departure, Hymenoptera, Diptera (more specifically Nematocera), Coleoptera and Oligochaeta were the most frequent recoveries. Within the region as a whole, ants were recovered from nearly half of all samples (.442), and diptera larvae from just under a third (.290). The highest frequencies per study area were diptera larvae at Strumble and Mwnt-Cemaes (.440 and .405 respectively), and ants from Newgale-Solva and Marloes (.774 and .425 respectively). These data may be related to seasonal influences by comparing the left-most 3 columns in Table 5.7 (see Section 5.3.3).

From the availability indices given in Tables 5.2 and 5.5, earthworms are the most prolific large-bodied prey, and, therefore, per organism, offer the best reward for the predator. However, the dipterous content given in Table 5.2, shows that tipulid (cranefly) larvae (=leatherjackets), with a body size comparable to smaller sized earthworms, have a high regional *AI* (.338) across the study range: from .309 at Mwnt-Cemaes to .386 at Marloes. Both these are subterranean prey giving no visual clues of presence and therefore will cost more energy to locate than the clumped and more visible dipterous and hymenopterous taxa, although these have smaller body sizes. Direct evidence with a telescope confirmed that dipterous larvae, especially tipulids, were taken throughout the year (*cf.* Table 5.7). No other family approaches the values for Lumbricidae and Tipulidae; even totalled indeterminate dipterous larvae have a mean value of only .073. The Bibionidae (in the same Nematocera suborder as the Tipulidae) is the only other family with a value >.03. It is interesting to note that in Mwnt-Cemaes, where land management emphasis is on pastoralism (4.3.4), Cyclorrhapha larvae (='maggots'), which

Table 5.7 Seasonal indices of frequency (feeding sites) and availability (Chough-used and unused areas) of invertebrate prey recovered in Welsh region (see Tables 5.2 - 5.4). Biological seasons: W = Winter (November-February), B = Breeding (March-June), PB = Post-breeding (July-October)

	Frequency in			Availability in					
	Feeding sites			Used areas			Unused areas		
Taxon	W	B	PB	W	B	PB	W	B	PB
OLIGOCHAETA	.344	.097	0	.598	.540	.612	.480	.894	1.571
ARACHNIDA	0	.125	.063	.001	.168	.273	.120	0	0
CRUSTACEA	.125	.097	.063	.274	.035	.347	.200	.064	0
DIPLOPODA	.125	.042	0	.137	.025	0	.080	0	0
CHILOPODA	.063	.014	0	.085	.064	.001	.120	0	0
DIPLURA	0	0	0	0	.001	0	0	0	0
DERMAPTERA	0	0	0	.077	.030	0	0	.064	0
ORTHOPTERA	0	.031	0	0	.173	.025	0	0	0
HEMIPTERA	0	0	0	0	<.001	0	0	0	0
LEPIDOPTERA	0	0	0	0	<.001	.025	0	0	0

Table 5.7 (continued)

DIPTERA									
Cyclorrhapha	.125	.014	.031	.060	.040	0	0	0	0
Nematocera	.219	.250	.063	.128	.718	.116	.160	.553	0
Brachycera	.094	.042	0	.026	.025	0	0	0	0
Indet. diptera	0	.125	0	.060	.094	.041	.040	0	0
All DIPTERA	.344	.361	.094	.282	.876	.248	.200	.553	0
HYMENOPTERA (ants)	.156	.403	.844	.214	.599	.612	.840	.106	0
COLEOPTERA									
Carabidae	.031	.042	.063	.231	.248	.085	.240	.159	.143
Hydrophilidae	0	.014	0	0	0	0	0	0	0
Silphidae	0	0	0	.001	.025	0	0	0	0
Staphylinidae	0	.042	0	.043	.064	.001	.040	0	0
Elateridae	0	.069	0	.094	.079	.025	.200	.064	0
Byrrhidae	0	.014	0	0	0	0	0	0	0
Meloidae	0	0	0	0	.015	0	0	0	0
Tenebrionidae	.063	0	0	.043	.064	0	.120	0	0
Scarabaeidae	.094	.139	.031	.026	.129	.058	.120	0	0
Indet. beetles	0	.014	0	<.001	<.001	.001	0	.021	0
All COLEOPTERA	.188	.278	.094	.453	.520	.182	.720	.213	.143
MOLLUSCA	0	0	0	0	.047	.058	0	.064	0
Total no. samples	32	72	32	117	202	121	25	47	7

include the dungflies, have an *AI* of .068 but are not represented in any of the remaining 3 study areas, nor were they found in the control sites at Mwnt-Cemaes. Evidence, however, was found in one faecal sample from Newgale-Solva (*cf.* Table 5.15). [Diptera larvae do not present well in faecal residue.]

Within the order Coleoptera, no single genus dominated, and certainly no species: only one carabid (*Amara aena*) was positively identified from 3 study areas; carabids of the genus *Harpalus* and tenebrionids of the genus *Cylindronotus* were identified from 2 areas each; *Athous* spp. (Elateridae) were also located from 2. Indeterminate scarabaeids, possibly *Aphodius*, were found in all 4 study areas; these are expected wherever ungulate dung is present, as are the Geotrupidae (adults of both families will also use carrion and fungi; and their larvae, apart from dung, will feed on humus and decomposing plant material (Ritcher 1958)). Coleopteran species diversity was greatest in Mwnt-Cemaes feeding areas, where ≥12 genera were identified; ≥10 were recorded at Newgale-Solva but abundances were greatly reduced, ≥8 from Strumble, but only 6 from Marloes (Tables 5.2 & 5.4), the only area with a Coleoptera *AI*<.10 (Table 5.2).

Among the other prey items recorded, woodlice were present in all feeding areas throughout the year, and were recovered from specific feeding points similarly. Faecal evidence suggests that they are taken outside the breeding season (5.3.5). With a very similar *AI*, spiders were probably preyed upon in the summer months when Wolf spiders (Lycosidae), crab spiders (Thomisidae) and harvestmen (Opilones) were common surface invertebrates. Additionally, millipedes (Diplopoda) and centipedes (Chilopoda) (=Myriapoda) were frequent and taken, especially at Newgale-Solva (*cf.* Table 5.15).

5.3.2 SIMILARITY COEFFICIENTS OF STUDY AREAS

Diversity is a crucial facet of ecological systems (Putman & Wratten 1984). In Section 4.3.4, it was stated that variation in habitat range justified the decision to choose more than one study area. Broadly speaking, of the 4 study areas selected, two, W1 and W2 (Mwnt-Cemaes and Strumble to the north) had an upland/pastoral/scrubby cliff physiography, whereas the two southern areas W3 and W4 (Newgale-Solva and Marloes) were more representative of lowland improved agriculture, though with better quality cliffs. It is possible to see from the data given in Tables 5.2 and 5.4, even though they under-represent the role of cereal grain, how this might affect Chough diet especially with regard to increased dependence on cereal and ants in the south, and earthworms, beetles and flies in the 'upland' areas. Mwnt-Cemaes showed the greatest diversity (Table 5.2) using Margalef's (1951) index:

$$D = \frac{S - 1}{\log_e N}$$

where D = index of diversity, S = number of groups or species, N = number of individuals. However, by applying Sorensen's (1948) quotient of similarity (QS):

$$QS = \frac{2j}{a + b}$$

where a = number of groups found in habitat A, b = number of groups found in habitat B, j = number of groups found in both habitats, the QS between the study areas were as follows (indeterminate taxa were excluded from equations):

W3/W4 = .560
W2/W4 = .558
W2/W3 = .471
W1/W4 = .444*
W1/W2 = .438
W1/W3 = .423

The study areas, grouped in all possible paired combinations have the following similarity quotients:

(W1+W4)/(W2/W3) = .506
(W1+W2)/(W3/W4) = .471*
(W1+W3)/(W2+W4) = .465

The study areas and values in bold type* represent pairs at the extremes (both geographically and agriculturally) of the study range, where least similarity was expected. Therefore, whatever the differences in the physiography of general areas of Chough usage, there is no apparent geographical pattern to the invertebrate similarity of the feeding areas sampled.

5.3.3 SEASONAL EFFECTS ON PREY AVAILABILITY

Seasonal effects on prey availability are shown in Table 5.7. The frequency at specific feeding points shows that in the winter, earthworms and fly larvae (mainly tipulids), both with a frequency index of .344, and beetles (.188) are the main invertebrate prey taxa (the exact role of cereal grain could not be accurately assessed within the same methodology, see Section 5.3.5). These are all relatively large-bodied organisms; the much smaller-bodied hymenopterans also have a surprisingly high value (.156), and the *AI* does not fall below .2 within used areas. The earthworm quotient falls off dramatically with the onset of the breeding season although availability within used areas remains high throughout the year. The dipterous quotient also remains high at feeding points before tailing off sharply in the post-breeding phase; however, availability does remain fairly high throughout the year, peaking in the summer at .876 due to a high Nematocera value: =.718 (see Section 5.4).

The hymenopterous quotient increases with the year, rising progressively from the winter low to a post-breeding high of .844, replacing, to some extent, the diptera. At feeding points, presence of fly larvae doubles in the post-breeding phase even though availability (as measured in used areas), does not increase significantly: remaining at the .600 mark. As already stated (4.3.3), ant activity can be found in most months of the year, and Choughs were observed to feed on them in November, December (in Cornwall) and February, although it is suggested later (5.4) that they are used primarily as a food for nestlings. Annually, presence of hymenopterans was highest at Newgale-Solva (.918: the highest value for any taxonomic group in any study area), it was lowest at Mwnt-Cemaes (.142) where increased availability of Diptera and Coleoptera is evident (.576 & .518 respectively). It is quite clear from Table 5.7 that Choughs are specifically selecting ant-rich areas during the breeding season: within used areas, ant availability rises throughout the year (.214-.599-.612) agreeing with the frequency trend in specific feeding sites (.156-.403-.844), whilst in nearby 'control' areas the availability trend is reversed (.840-.106-.000) (see Figure 5.4).

Similarly with the coleoptera resource, a large dip in availability occurs in control areas during the breeding season, although the difference is negligible during the post-breeding season. The Coleoptera quotient rises to a peak at feeding sites of .278 during the breeding season (Table 5.7); exactly half being accounted for by dung-beetles (Scarabaeidae). This tails off to a low level in the post-breeding phase when it is somewhat compensated for by increased usage of ground-beetles (Carabidae). From the coleopterous and dipterous evidence, both with a fairly low post-breeding frequency of .094, Choughs appear to move away from the typical prey of pasture to that associated with the natural clifflands, and this is in line with the evidence presented in Section 4.3.3 which shows that usage of the cliffs increases through the year (see also Section 6.4).

Figure 5.4

Seasonal change in the availability of ants in used and non-used areas, and the frequency of occurrence in feeding sites

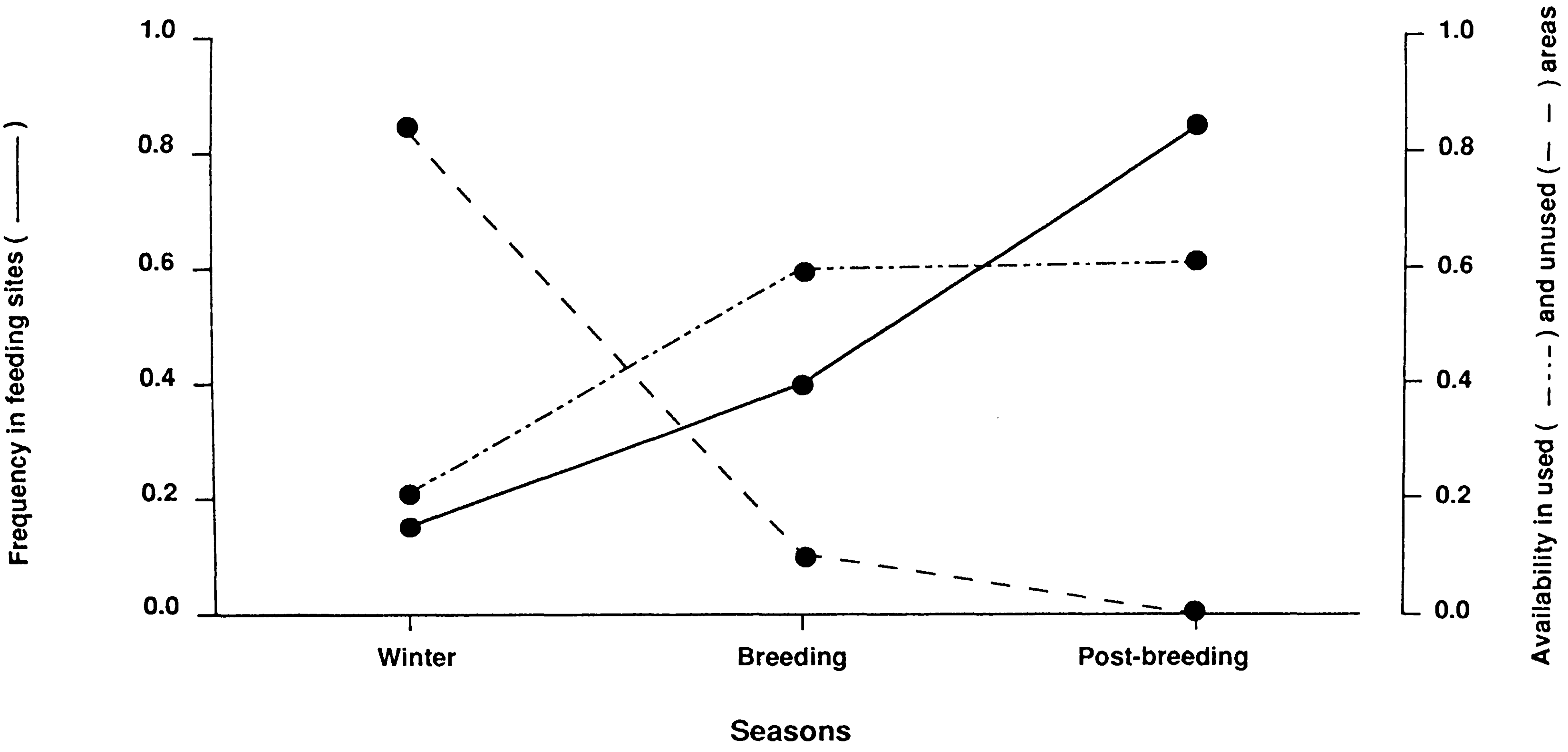

Frequency in feeding sites (———)
1.0
0.8
0.6
0.4
0.2
0.0
Winter
Breeding
Post-breeding
Seasons
Availability in used (—·-·—) and unused (— —) areas

Table 5.8 Taxa, source and index of availability of prey taxa recovered from potential Chough feeding sites in Cornish study areas*: 'I' = no. of individuals recovered (+ = minimum count) from 'S' (no. +ve samples); 'AI' = availability index; * see Section 2.3.3

	Availability in study areas									
	C1			C2			C3			Region
Taxon	I	S	AI	I	S	AI	I	S	AI	AI
OLIGOCHAETA										
'Small' lumbricidae	85	42	.857	51+	29	.711	35	21	.437	.677
'Medium' lumbricidae	54	40	.633	51+	19	.622	56+	29	.667	.641
Enchytraeids	93+	35	.864	34+	19	.468	14+	8	.167	.521
'Large' lumbricidae	6	5	.068	11	8	.162	14+	9	.175	.130
All OLIGOCHAETA	238+	79	2.129	147+	47	1.712	119+	44	1.262	1.724
ARACHNIDA										
Lycosidae	18	8	.170	4	3	.054	1	1	.008	.083
Indet. spiders	6	6	.075	7	7	.117	0	0	0	.062
Opilones (harvestmen)	3+	1	.020	3+	1	.027	0	0	0	.016
Thomisidae	0	0	0	1	1	.009	1	1	.008	.004
All ARACHNIDA	27	15	.265	15	12	.207	2	2	.016	.167
CRUSTACEA										
Indet. woodlice	0	0	0	22+	10	.279	10+	6	.119	.120
Philoscia muscorum	0	0	0	5	3	.063	6	3	.063	.039
Armadillidium vulgare	0	0	0	0	0	0	5	4	.063	.021
Metoponorthus cingendus	1	1	.007	2	1	.018	0	0	0	.008
Amphipoda sp.	0	0	0	6+	2	.063	0	0	0	.018
All CRUSTACEA	1	1	.007	35+	14	.405	21+	12	.238	.198

Table 5.8 (continued)

DIPLOPODA									
Indet. millipedes	3	3	.034	7	4	.090	1	1	.008	.042
Chordeumatida	0	0	0	1	1	.009	0	0	0	.003
Polydesmida	0	0	0	1	1	.009	0	0	0	.003
All DIPLOPODA	**3**	**3**	**.034**	**9**	**6**	**.108**	**1**	**1**	**.008**	.047
CHILOPODA										
Indet. centipedes	10	9	.122	6	5	.090	8	8	.119	.112
Geophilomorpha	1	1	.007	0	0	0	0	0	0	.003
All CHILOPODA	**11**	**10**	**.129**	**6**	**5**	**.090**	**8**	**8**	**.119**	.117
DIPLURA/COLLEMBOLA	**0**	**0**	**0**	**2**	**2**	**.027**	**1**	**1**	**.008**	.010
DERMAPTERA										
***Forficula* sp.**	**5+**	**3**	**.048**	**6**	**5**	**.090**	**0**	**0**	**0**	.044
ORTHOPTERA										
Indet. grasshoppers	**0**	**0**	**0**	**6+**	**2**	**.063**	**3+**	**1**	**.024**	.026
HEMIPTERA										
Indet. hemiptera	**2**	**2**	**.020**	**2**	**2**	**.027**	**2**	**2**	**.024**	.023
LEPIDOPTERA										
Pyralidae	1	1	.007	0	0	0	0	0	0	.003
Indet. Noctuidae	1	1	.007	0	0	0	0	0	0	.003
All Lepidoptera	**2**	**2**	**.020**	**0**	**0**	**0**	**0**	**0**	**0**	**.008**
DIPTERA										
CYCLORRHAPHA										
Scatophagidae	3+	1	.020	0	0	0	3+	1	.024	.016
Muscidae	0	0	0	4+	2	.045	0	0	0	.013
Calliphoridae	1	1	.007	3+	1	.027	0	0	0	.010
Rhagionidae	2	1	.014	0	0	0	0	0	0	.005
Drosphilidae	0	0	0	1	1	.009	0	0	0	.003
All CYCLORRHAPHA	6	3	.041	8+	3	.072	3+	1	.024	.044

Table 5.8 DIPTERA (continued)

NEMATOCERA										
Tipulidae	24+	15	.259	14	9	.198	0	0	0	.156
Mycetophilidae	4+	2	.034	3+	1	.027	0	0	0	.021
Bibionidae	0	0	0	3+	1	.027	0	0	0	.008
Sciaridae	0	0	0	2	1	.018	0	0	0	.005
Trichoceridae	1	1	.007	0	0	0	0	0	0	.003
Anispodia	0	0	0	0	0	0	1	1	.008	.003
All NEMATOCERA	**29+**	**18**	**.299**	**22+**	**11**	**.261**	**1**	**1**	**.008**	**.193**
BRACHYCERA										
Dolichopodidae	3	2	.027	0	0	0	0	0	0	.010
Threvidae	2	1	.014	0	0	0	0	0	0	.005
Empididae	1	1	.007	0	0	0	1	1	.008	.005
Asilidae	0	0	0	1	1	.009	1	1	.008	.005
Stratiomyidae	0	0	0	2	1	.018	0	0	0	.005
All BRACHYCERA	**6**	**4**	**.061**	**3**	**2**	**.036**	**2**	**2**	**.024**	**.031**
Indet. Diptera	**6**	**6**	**.075**	**8+**	**3**	**.072**	**3**	**2**	**.032**	**.065**
All DIPTERA	**47+**	**29**	**.463**	**41+**	**19**	**.450**	**9+**	**6**	**.079**	**.331**
HYMENOPTERA										
Lasius flavus	42+	15	.381	22+	8	.261	0	0	0	.221
Indet. *Myrmica*	6+	3	.054	3+	1	.027	15+	5	.151	.078
Lasius alienus	8+	3	.068	10+	4	.117	4+	2	.040	.073
Myrmica rubra	0	0	0	0	0	0	8+	3	.079	.026
Indet. ants	2	2	.014	3	2	.036	1	1	.008	.021
Myrmica sulcinodis	0	0	0	0	0	0	5+	2	.048	.016
Myrmica scabrinodis	3+	1	.020	0	0	0	2	1	.016	.013
Formicularia fusca	0	0	0	3+	1	.027	0	0	0	.008
Indet. Symphyta/sawflies	1	1	.007	0	0	0	1	1	.008	.005
Lasius fulginosus	1	1	.007	0	0	0	0	0	0	.003
(*Lasius* spp.	51	19	.456	32+	12	.378	4+	2	.040	.294
(*Myrmica* spp.	9	4	.075	3+	1	.027	30+	11	.294	.128
All HYMENOPTERA	**63**	**26**	**.558**	**41+**	**16**	**.468**	**36+**	**15**	**.349**	**.464**

Table 5.8 (continued)

COLEOPTERA									
CARABIDAE									
Indet. carabid	4	4	.048	3	2	.036	1	1	.008	.031
Leistus sp.	0	0	0	0	0	0	2	2	.024	.008
Pterostichus sp.	1	1	.007	1	1	.009	0	0	0	.005
Amara aena	0	0	0	0	0	0	1	1	.008	.003
Amara familiaris	1	1	.007	0	0	0	0	0	0	.003
Notiophylus hypocrita	1	1	.007	0	0	0	0	0	0	.003
Calathus sp.	1	1	.007	0	0	0	0	0	0	.003
Calathus melanocephalus	1	1	.007	0	0	0	0	0	0	.003
Nebria brevicollis	0	0	0	0	0	0	1	1	.008	.003
All CARABIDAE	**9**	**9**	**.082**	**4**	**3**	**.045**	**5**	**4**	**.040**	**.057**
HYDROPHILIDAE										
Cercyon haemorrhoidale	1	1	.007	0	0	0	0	0	0	.003
Sphaeridium scarabaeoides	0	0	0	0	0	0	1	1	.008	.003
All HYDROPHILIDAE	**1**	**1**	**.007**	**0**	**0**	**0**	**1**	**1**	**.008**	**.005**
SILPHIDAE										
***Silpha obscura* sp.**	**1**	**1**	**.007**	**0**	**0**	**0**	**0**	**0**	**0**	**.003**
STAPHYLINIDAE										
Indet. staphylinid	4	4	.048	2	2	.027	4+	2	.040	.039
Aleochara sp.	3	3	.034	0	0	0	0	0	0	.013
Philonthus laminatus	1	1	.007	3+	1	.027	0	0	0	.010
Philonthus varius	1	1	.007	1	1	.009	1	1	.008	.008
Philonthus sp.	2	2	.020	0	0	0	0	0		.008
Oxytelus laqueatus	0	0	0	3+	1	.027	0	0	0	.008
Philonthus fuscipanus	1	1	.007	1	1	.009	0	0	0	.005
Tachyporus hypnorum	1	1	.007	1	1	.009	0	0	0	.005
Tachyporus chrysomelinus	0	0	0	0	0	0	1	1	.008	.003
Creophilus sp.	1	1	.007	0	0	0	0	0	0	.003
Ocypus sp.	1	1	.007	0	0	0	0	0	0	.003
Quedius sp.	0	0	0	0	0	0	1	1	.008	.003
Staphylinus aencocephalus	0	0	0	0	0	0	1	1	.008	.003
All STAPHYLINIDAE	15	13	.129	11+	7	.108	8+	5	.063	.102

Table 5.8 COLEOPTERA (continued)

ELATERIDAE									
Agriotes sp.	13	11	.156	8+	5	.108	10	9	.143	.138
Athous haemorrhoidalis	3	3	0	5	4	.072	1	1	.008	.036
Indet. elaterid	2	2	.020	3	3	.045	1	1	.008	.023
Selatosomus aenus	5	4	.054	0	0	0	0	0	0	.021
Agriotes lineatus	4+	2	.034	0	0	0	1	1	.008	.016
Agriotes obscurus	2	2	.020	0	0	0	0	0	0	.008
Agrypus/Lacon murinus	1	1	.007	1	1	.009	1	1	.008	.008
Agriotes sputator	0	0	0	0	0	0	1	1	.008	.003
All ELATERIDAE	**30**	**25**	**.327**	**17+**	**12**	**.225**	**15**	**12**	**.167**	**.245**
BYRRHIDAE sp.	**0**	**0**	**0**	**1**	**1**	**.009**	**0**	**0**	**0**	**.003**
TENEBRIONIDAE										
Cylindronotus laevioctostriatus	7	6	.082	4	2	.045	8	5	.095	.076
Opatrum sabulosum	0	0	0	2	1	.018	0	0	0	.005
Cylindronotus striatus	0	0	0	1	1	.009	0	0	0	.003
All TENEBRIONIDAE	**7**	**6**	**.082**	**7**	**4**	**.072**	**8**	**5**	**.095**	**.083**
SCARABAEIDAE										
Indet. scarabid	21	15	.238	11+	7	.153	4+	2	.040	.148
Aphodius prodromus	1	1	.007	7+	3	.081	0	0	0	.026
Aphodius plagiatus	6+	2	.048	0	0	0	0	0	0	.018
A. punctato sulcutus	3+	1	.020	3+	1	.027	0	0	0	.016
Aphodius sp.	0	0	0	0	0	0	3+	1	.024	.008
Aphodius sphacelatus	3+	1	.020	0	0	0	0	0	0	.008
Aphodius ciratina	0	0	0	0	0	0	3+	1	.024	.008
Serica brunnea	0	0	0	1	1	.009	0	0	0	.003
All SCARABAEIDAE	**34+**	**18**	**.320**	**22+**	**10**	**.252**	**10+**	**3**	**.079**	**.221**
CHRYSOMELIDAE										
Indet. chrysomelid	0	0	0	1	1	.009	0	0	0	.003
Sermylessa halensis	1	1	.007	0	0	0	0	0	0	.003
All CHRYSOMELIDAE	**1**	**1**	**.007**	**1**	**1**	**.009**	**0**	**0**	**0**	**.005**

Table 5.8 COLEOPTERA (continued)

CURCULIONIDAE										
Hypera sp.	2	2	.020	0	0	0	0	0	0	.008
Sitona waterhousei	0	0	0	1	1	.009	0	0	0	.003
Indet. weevil	2	2	.020	1	1	.009	1	1	.008	.013
All CURCULIONIDAE	4	4	.041	2	2	.018	1	1	.008	.023
Indet. beetles	1	1	.007	1	1	.009	2	2	.024	.013
All COLEOPTERA	103+	63	1.007	66+	30	.748	50	28	.484	.760
GASTROPODA										
Indet. slug	3	3	.034	9	8	.144	0	0	0	.055
Indet. snail	0	0	0	1	1	.009	0	0	0	.003
Nemoralis sp.	0	0	0	0	0	0	1	1	.008	.003
All GASTROPODA	3	3	.034	10	9	.153	1	1	.008	.060
INDETERMINATE TAXA	1	1	.007	0	0	0	0	0	0	.003
Diversity index *D*	24.8			23.2			20.4			34.3
Total no. samples	147			111			126			384

Diversity index after Margalef (1951), see text p. 128

5.3.4 COMPARISON OF PREY AVAILABILITY IN WALES AND CORNWALL

The results of 384 soil samples collected from potential Chough-feeding areas in Cornwall over all seasons in 1988 are given in Table 5.8. The rankings of the most important vertebrate taxa (*AI* >.10) are almost the same as in the Welsh feeding areas shown in Table 5.2 (Table 5.9); with only Coleoptera and Diptera reversing positions. Some of the values (availability) differ considerably, notably Oligochaeta and Coleoptera but most of the taxonomic groups are remarkably similar. A Mann-Whitney *U*-test revealed no significant difference in ranks between the 2 regions (*U*=54.5, d.f.10) over the wider prey spectrum but, as shown in Table 5.9, all except one of the most important 7 groups had a greater availability in Cornwall, although one other (Hymenoptera) was effectively tied with a difference of only .001. The respective availability of all groups is shown in Figure 5.5. The diversity in Cornwall at *D*=34.3 was nearly 8 points greater than the Welsh value.

Table 5.9 Summary of ranks of main prey taxa in Cornwall (*AI* >.1) and respective positions in Wales with difference in Availability index (- = greater in Wales)

Rank	Taxon	Rank in Wales	Regional difference
1	OLIGOCHAETA	1	1.171
2	COLEOPTERA	4	0.424
3	HYMENOPTERA	3	0.001
4	DIPTERA	2	-0.168
5	CRUSTACEA	5	0.039
6	ARACHNIDA	6	0.029
7	CHILOPODA	7	0.067

Figure 5.5

Comparative availability of invertebrate prey in Wales and Cornwall in feeding areas (Wales N = 441) and potential feeding areas (Cornwall N = 384). Left hand (shaded) section of bars represents Welsh values. Aggregated values for Diptera and Coleoptera families are also shown in same format

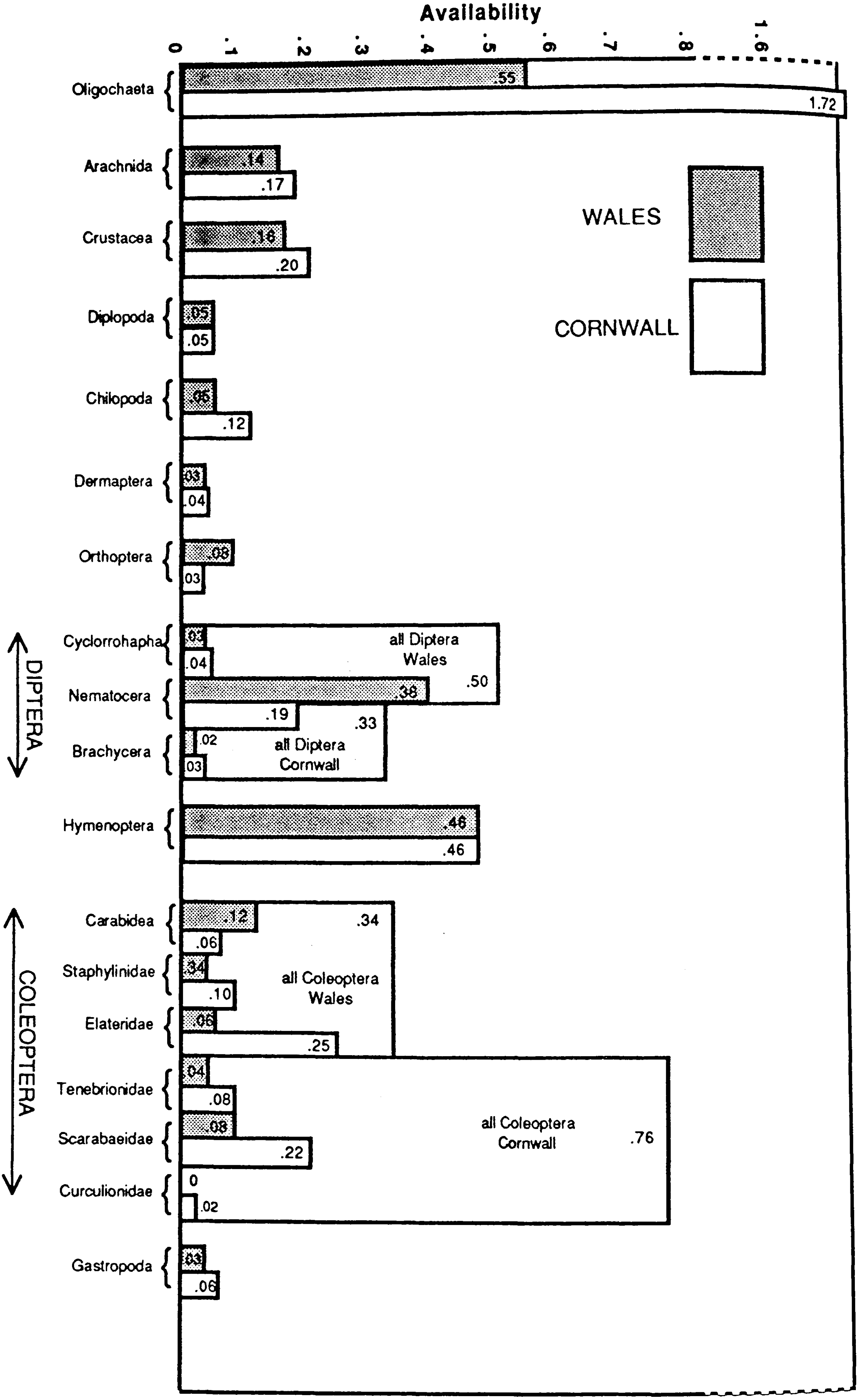

Availability
0
.1
.2
.3
.4
.5
.6
.7
.8
1.6
WALES
CORNWALL
Oligochaeta
.55
1.72
Arachnida
.14
.17
Crustacea
.16
.20
Diplopoda
.05
.05
Chilopoda
.06
.12
Dermaptera
.03
.04
Orthoptera
.08
03
DIPTERA
Cyclorrohapha
.03
.04
all Diptera Wales
.50
Nematocera
.38
.19
.33
Brachycera
.02
03
all Diptera Cornwall
Hymenoptera
.46
.46
COLEOPTERA
Carabidea
.12
.06
.34
Staphylinidae
34
.10
all Coleoptera Wales
Elateridae
.06
.25
Tenebrionidae
.04
.08
Scarabaeidae
.08
.22
all Coleoptera Cornwall
.76
Curculionidae
0
.02
Gastropoda
.03
.06

Table 5.10 Taxa, source and index of availability of prey taxa recovered from control sites adjacent to potential feeding sites in Cornish study areas: 'I' = no. of individuals (+ = minimum count) recovered from 'S' (no. +ve samples); 'AI' = availability index

	Availability in study areas									
	C1			C2			C3			Region
Taxon	I	S	AI	I	S	AI	I	S	AI	AI
OLIGOCHAETA										
'Small' lumbricidae	58	20	1.925	4	3	.500	29	21	.681	1.065
'Medium' lumbricidae	44	20	1.575	16+	7	1.833	58	33	1.250	1.411
Enchytraeids	22	9	.750	6	4	.750	3	2	.056	.347
'Large' lumbricidae	5	5	.225	0	0	0	11	7	.236	.210
All OLIGOCHAETA	**129**	**54**	**4.475**	**26+**	**10**	**2.750**	**101**	**41**	**1.917**	**2.823**
ARACHNIDA										
Indet. spiders	2	2	.075	0	0	0	1	1	.014	.032
Lycosidae	1	1	.025	0	0	0	1	1	.014	.016
Thomisidae	0	0	0	1	1	.083	0	0	0	.008
Tetragnathidae	0	0	0	0	0	0	1	1	.014	.008
All ARACHNIDA	**3**	**3**	**.125**	**1**	**1**	**.083**	**3**	**3**	**.042**	**.065**
CRUSTACEA										
Indet. woodlice	0	0	0	5	2	.500	13	7	.264	.202
Armadillidium vulgare	0	0	0	0	0	0	8	7	.194	.113
Philoscia muscorum	0	0	0	0	0	0	9	4	.167	.097
All CRUSTACEA	**0**	**0**	**0**	**5**	**2**	**.500**	**30**	**14**	**.569**	**.379**
DIPLOPODA										
Indet. millipedes	1	1	.025	2	1	.167	7	3	.125	.097
Chordeumatida	0	0	0	0	0	0	1	1	.014	.008
All DIPLOPODA	**1**	**1**	**.025**	**2**	**1**	**.167**	**8**	**4**	**.139**	**.105**

Table 5.10 (continued)

CHILOPODA										
Indet. centipedes	4	4	.175	0	0	0	3	3	.069	.097
Geophilomorpha	2	1	.050	0	0	0	0	0	0	.016
All CHILOPODA	6	5	.225	0	0	0	0	0	0	.113
DIPLURA/COLLEMBOLA	0	0	0	1	1	.083	2	2	.042	.032
ORTHOPTERA										
Indet. grasshoppers	0	0	0	0	0	0	3+	1	.042	.024
HERMIPTERA										
Indet. hermiptera	0	0	0	0	0	0	5+	2	.083	.048
LEPIDOPTERA										
Indet. moth	1	1	.025	0	0	0	0	0	0	.008
DIPTERA										
CYCLORRHAPHA										
Calliphoridae	0	0	0	1	1	.083	0	0	0	.008
Chloropidae	0	0	0	0	0	0	1	1	.014	.008
All CYCLORRHAPHA	0	0	0	1	1	.083	1	1	.014	.016
NEMATOCERA										
Tipulidae	3	3	.125	1	1	.083	0	0	0	.048
Mycetophilidae	0	0	0	0	0	0	1	1	.014	.008
Bibionidae	1	1	.025	0	0	0	0	0	0	.008
All NEMATOCERA	4	4	.150	1	1	.083	1	1	.014	.065
BRACHYCERA										
Empididae	1	1	.025	0	0	0	0	0	0	.008
Indet. Diptera	0	0	0	1	1	.083	1	1	.014	.016
All DIPTERA	5	5	.175	3	2	.250	3	3	.042	.105
HYMENOPTERA										
Indet *Myrmica*	0	0	0	0	0	0	1	1	.014	.008

COLEOPTERA										
CARABIDAE										
Harpalus aenus	0	0	0	0	0	0	1	1	.014	.008
Badister bipustulatus	0	0	0	0	0	0	1	1	.014	.008
Amara tibialis	0	0	0	4	2	.417	0	0	0	.040
Agonum muelleri	1	1	.025	0	0	0	0	0	0	.008
Bembidion lunulatum	1	1	.025	0	0	0	0	0	0	.008
All CARABIDAE	2	2	.050	4	2	.417	2	2	.028	.073
STAPHYLINIDAE										
Quedius sp.	1	1	.025	0	0	0	0	0	0	.008
Philonthus sp.	1	1	.025	0	0	0	0	0	0	.008
Indet. staphylinid	0	0	0	1	1	.083	1	1	.014	.016
All STAPHYLINIDAE	2	2	.050	0	0	0	0	0	0	.032
ELATERIDAE										
Agriotes sp.	2	2	.075	0	0	0	3	3	.069	.065
Indet. elaterid	3	2	.100	0	0	0	1	1	.014	.040
Athous haemorrhoidalis	1	1	.025	0	0	0	1	1	.014	.016
Agriotes acuminatus	1	1	.025	0	0	0	0	0	0	.008
All ELATERIDAE	7	6	.225	0	0	0	5	4	.083	.129
DASCILLIDAE										
Dascillus corvinus	0	0	0	0	0	0	1	1	.014	.008
SCARABAEIDAE										
Aphodius sp.	3+	1	.107	0	0	0	0	0	0	.024
Indet. scarab.	1	1	.025	0	0	0	0	0	0	.008
All SCARABAEIDAE	4+	2	.100	0	0	0	0	0	0	.032
CURCULIONIDAE										
Indet. weevil	0	0	0	0	0	0	2	2	.042	.024
CANTHARIDAE										
Cantharus sp.	1	1	.025	0	0	0	0	0	0	.008
Indet. beetles	0	0	0	0	0	0	3+	1	.042	.024
All COLEOPTERA	16	13	.450	5	3	.500	14+	11	.222	.331
GASTROPODA										
Indet. snail	0	0	0	0	0	0	1	1	.014	.008
Diversity index *D*		10.4			6.7			12.9		17.4
Total no. samples		40			12			72		124

Diversity index after Margalef (1951), see text p. 128

In Cornwall it was necessary to select areas which were, based on Welsh observations, apparently suitable for Choughs. This could, of course, have caused bias. In an effort to reduce this factor, contiguous areas were also chosen, as in Wales, which were apparently less slightly suitable (*e.g.* with longer vegetation). The results are given in Table 5.10, and summarised in Table 5.11 with the respective positions and differences in Wales (comparative data from Table 5.3). Again Cornwall is shown to be more diverse with a greater abundance of most prey groups, with earthworms being very much more abundant. Only with Hymenoptera did Wales show an appreciably greater abundance. Perhaps no undue significance should be read into these results because of the subjective nature of the habitat selection. Table 5.12 gives the seasonal breakdown for those Cornish sites which were selected as being equivalent of the used areas in Wales (*cf*. Table 5.7). Interestingly, the hymenoptera, possibly crucial while rearing young (see Section 5.4), have

Table 5.11 Summary of ranks of potential prey taxa in Cornwall and respective rankings in Wales with difference in *AI* ('-' =greater in Wales)

Rank	Taxon	Rank in Wales	Regional difference
1	OLIGOCHAETA	1	1.886
2	CRUSTACEA	5	0.278
3	COLEOPTERA	3	0.015
4	CHILOPODA	6=	0.075
5	DIPTERA	2	0.338
6	DIPLOPODA	10	0.080
7	ARACHNIDA	6=	0.027
8	ORTHOPTERA	11	0.024
9	HYMENOPTERA	4	-0.296
10	GASTROPODA	6=	-0.030
11	DERMAPTERA	6=	-0.038

Table 5.12 Seasonal indices of availability in potential Chough areas of prey recovered in Cornish region (see Tables 5.8). Biological seasons: W = Winter (November-February), B = Breeding (March-June), PB = Post-breeding (July-October)

Taxon	Availability in Potential feeding sites		
	W	B	PB
OLIGOCHAETA	2.217	1.679	1.271
ARACHNIDA	.031	.126	.365
CRUSTACEA	.054	.365	.083
DIPLOPODA	.023	.057	.031
CHILOPODA	.178	.063	.073
DIPLURA	.008	0	.021
DERMAPTERA	.031	.069	0
ORTHOPTERA	0	.044	.031
HERMIPTERA	0	.044	.010
LEPIDOPTERA	0	.006	.010
DIPTERA			
Cyclorrhapha	.078	.044	0
Nematocera	.147	.314	.010
Brachycera	.039	.031	.021
Indet. diptera	.047	.088	.031
All DIPTERA	.310	.478	.062
HYMENOPTERA	.256	.591	.417
COLEOPTERA			
Carabidae	.054	.038	.073
Hydrophilidae	0	.006	.010
Silphidae	0	.006	0
Staphylinidae	.062	.138	.083
Elateridae	.248	.245	.146
Byrrhidae	.008	0	0
Tenebrionidae	.109	.057	.042
Scarabaeidae	.178	.358	.063
Chrysomelidae	0	.006	.010
Curculionidae	.008	.031	.010
Indet. beetles	0	.038	0
All COLEOPTERA	.667	.868	.448
MOLLUSCA	.016	.075	.063
OTHER	0	0	.010
Total no. samples	129	159	96

very similar *AI's* in the two regions during the breeding season (a difference of only .008). On the other hand, the Lizard region, which scores poorest of the 3 Cornish study areas (although still richer than any Welsh site) in areas rated as prime potential Chough feeding areas, is richest in the adjacent believed less suitable areas. It is possible to conclude that a slight shift in choice criteria of Cornish habitats (or in management) would affect the diversity indices given in Table 5.8. Nevertheless, the indices of the Cornish sites are all, bar one, greater than the Welsh counterparts: the exception is Mwnt-Cemaes, which reaches a higher value than West Penwith only. The index for the Cornish region (17.4) is more than 4 points greater than Wales (13.3). However, as mentioned already (5.2.2), diversity might be less important than abundance/availability of a few key species, such as ants, at critical times of the year (see Section 5.4).

5.3.5 FAECAL SAMPLING

A total of 449 faecal samples, including 15 cast pellets from Cornwall, were collected. Of these 335 (75%) were of Welsh origin (Table 5.13). In overview, most of the groups noted by Goodwin (1986) as food items were recovered (Table 5.14) and a number of additional finds were made (Table 5.15). Earwigs, the ubiquitous *Forficula auricularia*, formed a varying proportion of the prey items, up to 15%, at all main study areas despite a low recovery rate from feeding area soil cores (*cf.* Table 5.2). In contrast, the Orthoptera, noted by Goodwin (*ibid*) as prey, were represented only by a single ootheca of the Cockroach *Ectobius* sp.

Table 5.13 Numbers and sources of faecal and pellet samples

Area	Region	No.
W1 Mwnt-Cemaes	Dyfed	108
W2 Strumble	"	39
W3 Newgale-Solva	"	66
W4 Marloes	"	64
Rame peninsula	Cornwall	114*
Ramsey Island	Dyfed	49
Stackpole	"	9
Total		449

* includes 15 pellets

The overall impression is that the birds take relatively poorly mobile, even sessile, prey. Only one adult dipteran was recovered, the Yellow dung-fly *Scatophaga stercoraria*, which may have been consumed within its puparium whilst the bird was turning over dung, from which much of the fauna comes. Dipterous larvae, however, are much more frequent, occurring in >1/3 of the samples from the two northern, more pastoral study areas (Table 5.15). These included many tipulid head capsules. Other Diptera are represented by unidentifiable puparial fragments and parts of the puparium of the muscid *Morellia* cf. *hortorum*, which breeds in dung (Skidmore 1985). It is very probable that the value for dipterous larvae is an underestimate in that this is one element in the Chough's diet of which no identifiable part survives digestion well. The presence of wing fragments, sometimes identifiable to species level, implies that imagines of Diptera would have been recognisable had they been regularly taken.

Coleopterous evidence, as both larvae and adults (Table 5.16), is remarkably frequent, occurring in 84% of all Welsh samples: in >3/4 of

Table 5.14 Seasonal frequency of prey (all ages) in West Wales as represented by percentage occurrence of remains in faecal samples; summary of Table 5.15

	% Frequency in region			
	Season			Year
Taxon	W	B	PB	
OLIGOCHAETA	29	10	20	20
ARACHNIDA	3	3	0	2
CRUSTACEA	3	0	4	2
MYRIAPODA	4	1	2	3
DERMAPTERA	9	10	4	8
ORTHOPTERA	0	0	2	-
HEMIPTERA	1	2	0	1
LEPIDOPTERA	1	4	2	2
DIPTERA	15	49	18	29
HYMENOPTERA	4	0	36	9
COLEOPTERA (all)	81	89	95	84
Carabidae	37	30	62	39
Staphylinidae	11	4	22	10
Elateridae	1	16	0	6
Tenebrionidae	4	9	13	8
Scarabaeidae/Geotrupidae	12	37	24	24
Curculionidae	13	15	9	13
Other families	5	7	5	3
Indet. beetles	36	15	5	22
CEREAL GRAIN	49	2	9	23
OTHER	3	2	0	2
Total no. samples	117	105	55	277

Table 5.15 Prey as represented by remains in faecal samples. Percentage seasonal frequency of occurrence (positive samples/total samples) in Welsh study areas. Age: indeterminate full-grown except where stated: A =adults, L =larvae; seasons: W =winter (November-February), B =breeding (March-June), PB =post-breeding (July-October), Y = all year

	% Frequency in study area															
	W1				W2				W3				W4			
Taxon	W	B	PB	Y	W	B	PB	Y	W	B	PB	Y	W	B	PB	Y
OLIGOCHAETA	7	8	33	12	56	10	50	31	64	9	9	27	18	25	50	20
ARACHNIDA indet. spiders	3	0	0	1	0	5	0	3	5	18	0	5	0	0	0	0
Indet. Opilones	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
CRUSTACEA indet. woodlice	0	0	11	2	0	0	0	0	0	0	0	0	8	0	0	6
MYRIAPODA	0	0	0	0	0	5	0	3	23	0	3	9	0	0	0	0
DERMAPTERA *Forficula* sp.	3	10	0	8	19	10	50	15	9	18	3	8	6	0	0	5
ORTHOPTERA Blattidae																
Ectobius sp.	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
HEMIPTERA (A)																
Coreidae *Enoplops scapha*	0	0	0	0	0	5	0	3	0	0	0	0	0	0	0	0
Pentatomidae *Dolycornis baccorum*	0	0	0	0	0	0	0	0	0	9	0	2	0	0	0	0
LEPIDOPTERA (L)	0	5	0	3	0	5	0	3	0	0	3	2	2	0	0	2
DIPTERA (L, all)	21	48	28	37	6	62	0	36	9	27	15	15	18	50	0	23
NEMATOCERA																
Tipulidae	14	41	17	30	0	62	0	33	9	27	12	14	16	42	0	20
Bibionidae	3	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0
BRACHYCERA Tabanidae	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
CYCLORRHAPHA Phoridae	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
Indet. diptera	3	2	11	4	6	0	0	3	0	0	0	0	0	8	0	2

Table 5.15 (continued)

HYMENOPTERA (A, all)	0	0	44	7	0	0	0	0	18	0	36	24	2	0	0	2
Lasius flavus	0	0	28	5	0	0	0	0	0	0	15	8	2	0	0	2
Lasius niger	0	0	0	0	0	0	0	0	0	0	6	3	0	0	0	0
Myrmica sp.	0	0	0	0	0	0	0	0	9	0	12	9	0	0	0	0
Myrmica scabrinodis	0	0	0	0	0	0	0	0	9	0	6	6	0	0	0	0
Indet. ants	0	0	17	3	0	0	0	0	0	0	0	0	0	0	0	0
Indet. Symphyta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COLEOPTERA (all)	66	89	83	81	81	76	100	79	95	100	100	98	70	100	100	77
CARABIDAE (all)	48	31	72	43	19	29	0	23	59	45	65	61	26	17	0	23
Agonum sp. (A)	0	0	11	2	0	0	0	0	0	0	0	0	0	0	0	0
Agonum dorsale (A)	7	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Amara sp. (A)	0	5	6	4	6	10	0	8	5	27	6	9	12	17	0	13
Amara aenea (A)	0	0	0	0	0	0	0	0	14	0	0	5	0	0	0	0
Amara similata (A)	0	0	0	0	6	0	0	3	0	0	0	0	0	0	0	0
Amara tibialis (A)	0	0	0	0	0	0	0	0	9	0	3	5	0	0	0	0
Bembidion lampros (A)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	3
Calathus erratus (A)	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
Calathus fuscipes (A)	0	0	0	0	0	0	0	0	0	0	9	5	0	0	0	0
Carabus problematicus (A)	0	0	0	0	0	0	0	0	0	0	6	3	0	0	0	0
Cychrus caraboides (A)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Harpalus sp. (A)	0	0	0	0	0	0	0	0	0	9	3	3	0	0	0	0
Harpalus affinis (A)	0	0	11	2	0	0	0	0	0	9	0	2	0	0	0	0
Loricera pilicornis (A)	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Nebria sp. (A)	0	0	11	2	0	0	0	0	0	0	0	0	0	0	0	0
Pterostichus sp. (A)	0	0	0	0	0	0	0	0	5	9	24	15	2	0	0	2
Pterostichus ?madidus (A)	0	0	0	0	0	0	0	0	0	0	9	5	0	0	0	0
Trechus obtusus (A)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Indet. (A)	17	7	33	14	6	0	0	3	18	9	15	15	4	0	0	3
Indet. (L)	31	21	0	20	0	19	0	10	18	0	0	6	0	0	0	0
HYDRAENIDAE *Helophorus* sp. (A)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	3
HYDROPHILIDAE (A)																
Cercyn sp.	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	3
Hydrobius fuscipes	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2

Table 5.15 COLEOPTERA (continued)

SILPHIDAE (A)																
Silpha sp.	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
Thanatophilis sp.	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
STAPHYLINIDAE (all)	3	5	0	4	0	0	50	3	18	0	33	23	16	8	0	14
Philonthus sp. (A)	0	0	0	0	0	0	0	0	5	0	0	2	6	0	0	5
Staphylinus sp. (A)	0	0	0	0	0	0	0	0	5	0	18	11	2	8	0	3
Staphylinus sp. (L)	0	0	0	0	0	0	0	0	5	0	3	3	0	0	0	0
S. ?aenocephalus (A)	0	0	0	0	0	0	0	0	0	0	9	5	4	0	0	3
Stenus sp. (A)	0	0	0	0	0	0	0	0	5	0	0	2	0	0	0	0
?Ocypus olens (A)	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
Indet. (A)	0	0	0	0	0	0	50	3	5	0	0	2	4	0	0	3
Indet. (L)	3	5	0	4	0	0	0	0	0	0	0	0	0	0	0	0
ELATERIDAE (all)	3	18	0	11	0	5	0	3	0	18	0	3	0	25	0	5
Indet. (A)	0	11	0	6	0	0	0	0	0	0	0	0	0	0	0	0
Indet. (L)	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Agriotes sp. (A)	3	2	0	2	0	5	0	3	0	0	0	0	0	8	0	2
Agriotes ?obscurus (A)	0	0	0	0	0	0	0	0	0	9	0	2	0	0	0	0
Agrypus murinus (A)	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	2
Athous sp. (A)	0	2	0	1	0	0	0	0	0	9	0	2	0	8	0	2
TENEBRIONIDAE (all)	0	2	0	1	0	10	0	5	23	55	21	27	0	0	0	0
Cylindronotum sp.	0	2	0	1	0	0	0	0	18	0	0	6	0	0	0	0
C. laevioctostriatus (A)	0	0	0	0	0	10	0	5	0	0	0	0	0	0	0	0
Opatrum sabulosum	0	0	0	0	0	0	0	0	5	55	21	21	0	0	0	0
SCARABAEIDAE/GEOTRUPIDAE (all)	3	30	22	21	0	10	50	8	5	82	18	24	24	83	100	38
Aphodius sp. (A)	0	23	6	14	0	5	0	3	5	27	0	6	12	42	100	20
Aphodius sp. (L)	0	5	0	3	0	0	0	0	0	9	0	2	0	0	0	0
Aphodius contaminatus (A)	0	0	6	1	0	0	0	0	0	0	0	0	0	0	0	0
Aphodius sphacelatus (A)	0	0	6	1	0	0	0	0	0	0	0	0	4	8	0	5
Aphodius rufipes (A)	0	0	0	0	0	5	0	3	0	27	12	11	0	0	0	0
Aphodius rufipes (L)	0	0	0	0	0	0	0	0	0	0	0	0	4	33	0	9

Table 5.15 COLEOPTERA SCARABAEIDAE (continued)

Cetonia sp. (A)	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
Cetonia aurata (A)	0	0	0	0	0	0	0	0	0	0	0	0	2	8	0	3
Geotrupes sp. (A)	0	2	6	2	0	0	50	3	0	0	6	3	2	8	0	3
Onthophagus sp. (A)	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	2
Onthophagus similis (A)	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus joannae (A)	0	0	0	0	0	0	0	0	0	18	0	3	0	0	0	0
Indet. (A)	0	0	11	2	0	0	0	0	0	0	0	0	0	0	0	0
Indet. (L)	3	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
CURCULIONIDAE (all)	0	7	11	6	13	24	0	18	14	36	9	15	20	25	0	20
Barypeithes ?pellucidus (A)	0	0	0	0	0	0	0	0	0	9	0	2	0	0	0	0
Notaris bimaculatus (A)	0	0	0	0	13	0	0	5	0	0	0	0	0	0	0	0
Otiorhynchus ligneus (A)	0	0	3	1	0	5	0	3	9	9	3	6	12	8	0	11
?*Phytonomous* sp. (A)	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Sitona sp. (A)	0	2	0	1	0	5	0	3	0	0	0	0	2	0	0	2
Sitona ?cylindricollis (A)	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Sitona hispidulus (A)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	3
Trachyploeus sp. (A)	0	0	0	0	0	5	0	3	5	0	0	2	0	0	0	0
Indet. (A)	0	3	3	3	0	14	0	8	0	18	6	6	0	17	0	3
Indet. beetles (A)	66	10	0	23	50	10	0	26	18	18	9	14	10	8	0	9
Indet. beetles (L)	14	7	0	7	6	5	0	5	0	0	0	0	2	0	0	2
GASTROPODA																
Bivalvia																
Mytilus edulis	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Endodontidae																
Discus rotundatus	0	0	0	0	0	0	0	0	5	0	0	2	0	0	0	0
CEREAL GRAIN	34	0	6	10	25	0	0	10	14	0	12	11	80	17	0	67
INDET. FRAGMENTS	0	0	0	0	19	0	0	8	0	0	0	0	0	8	0	2
Total no. samples	29	61	18	108	16	21	2	39	22	11	33	66	50	12	2	64

Table 5.16 Proportions of adult and larval Coleoptera present within the faecal evidence (n=no. of samples with beetle evidence) in Wales (all seasons) and Cornwall (winter only)

	Wales (n=233)		Cornwall (n=67)	
Taxon	Adults	Larvae	Adults	Larvae
Carabidae	.36	.13	.43	.06
Staphylinidae	.10	.02	0	0
Elateridae	.06	.01	0	0
Tenebrionidae	.09	0	.30	0
Scarabaeidae/Geotrupidae	.25	.06	.48	0
Curculionidae	.15	0	.06	0
Other	.22	.05	.04	0
All	.88	.24	.97	.06

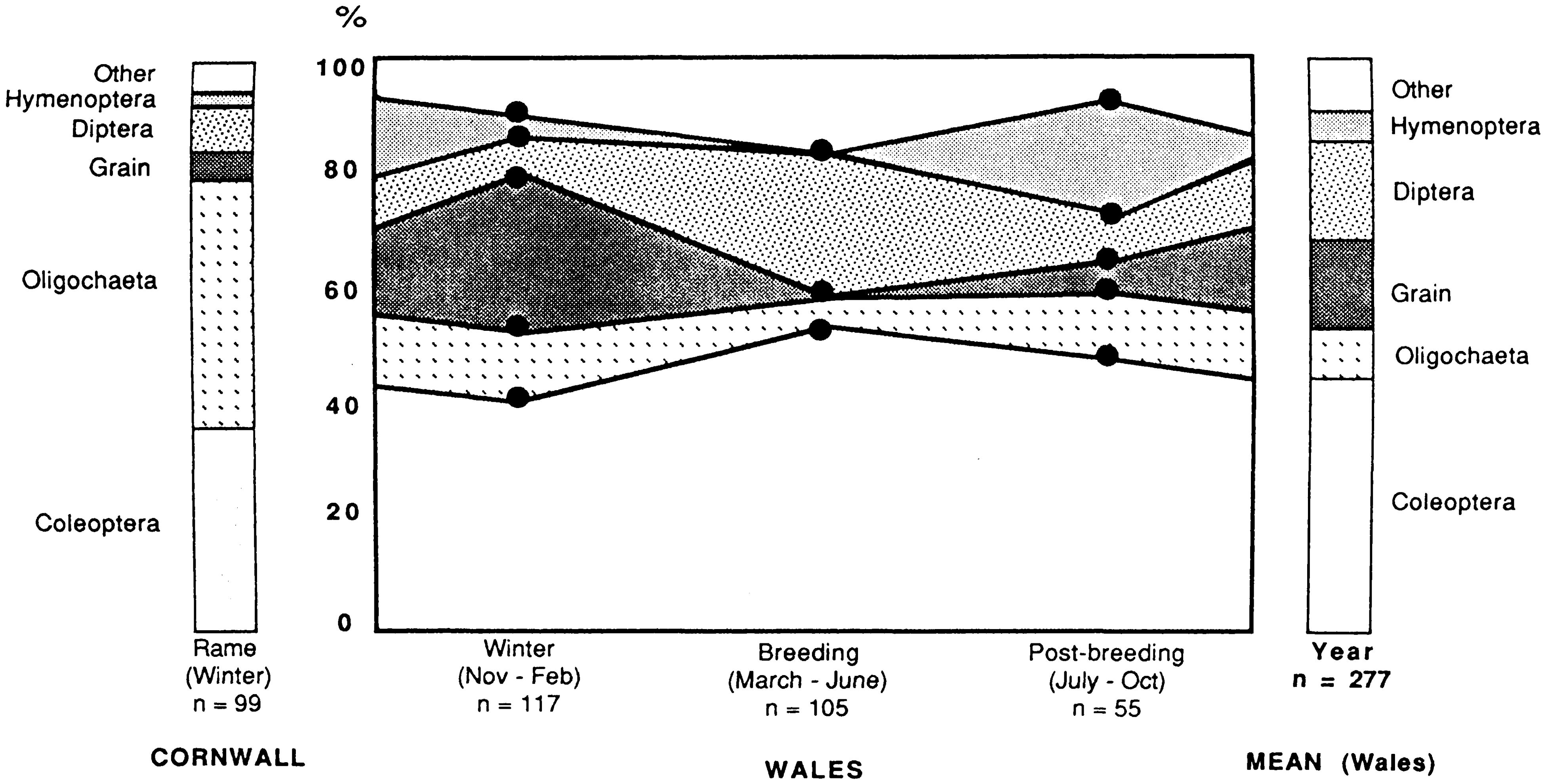
those from each main study area, and in all but one of 66 from Newgale-Solva. Many of the taxa would have been obtained from beneath dung or by turning stones (as might the earwigs), in particular, carabid ground beetles and their larvae, whilst many others, including elaterid click beetles would have been taken by searching in pasture, where they can occur at densities of 2-3 million/acre (Wallwork 1976). Numerically, in the evidence, the dung beetles (Geotrupidae/Scarabaeidae), as imagines and larvae, are exceeded only by the ground beetles. Since *Aphodius rufipes* largely hibernates as a third instar larva, and *A. spacelatus* as an imago, it is not surprising that they appear thus in faeces during the winter (Tables 5.15 & 5.18). Some carabids, including *Carabus problematicus*, *C. violaceus* and *Nebria brevicollis* mate in late summer and autumn; the winter populations of these too is composed mainly of developing larvae and pupae (Wallwork 1970). Other carabids have an early activity peak in spring/early summer, and a late one in late summer/autumn; species which mate and oviposit early, overwinter as adults (*ibid.*).

Table 5.15 gives the seasonal variations for all taxa in the Welsh assemblage; these data are summarised in Table 5.14 and Figure 5.6.

Whilst the majority of the fauna appears to have been taken from well-grazed rough pasture, there is also a significant element from other habitats. The number of *Opatrum sabulosum* (from Newgale-Solva (W3) throughout the year and from Rame in Cornwall in the winter) was unexpected. Brendell (1975) does not record the species from Cornwall, although in faecal samples collected there, it occurred in 17% of 99 samples (Table 5.18; it is found in sandy or 'waste' areas, principally on the coast (*ibid*, Harde 1984), at the roots of plants (Brendell 1975), and will burrow in dry, sandy grassland (R. Crowson pers. comm.). The absence of common sand-dune species is due to the rocky nature of the study coastline. The large ground beetle *Cychrus caraboides* is regarded by Lindroth (1973) as primarily a woodland species, only occurring in open country in mountain areas, although it has been found feeding upon snails on the machair of the Outer Hebrides (P. Buckland pers comm.). It is the only predominantly woodland element noted in the Chough's diet, although too much emphasis should not be placed upon a single individual, which may reflect a chance capture of a migrating animal. There is sufficient in the assemblage to infer some hunting along the edge of wetlands, possibly scavenged while drinking; Choughs were once recorded from such a habitat at Strumble, and this is the habitat where the curculionid (weevil) *Notaris bimaculatus* will occur on aquatic sedges (Cyperaceae). The hydrophilid *Hydrobius fuscipes* might similarly have been taken from adjacent to Marloes Mere (W4). Weevils, though featuring prominently in faecal samples and also in some collected in the Stackpole area (Haycock & Meyer 1988), were not encountered during routine live sampling (see Tables 5.2 - 5.4).

Figure 5.6

Adult Chough diet in Wales and Rame, Cornwall (winter) as indicated by the percentage seasonal occurrence of detectable faecal evidence


%
100
80
60
40
20
0
Other
Hymenoptera
Diptera
Grain
Oligochaeta
Coleoptera
Rame
(Winter)
n = 99
CORNWALL
Winter
(Nov - Feb)
n = 117
Breeding
(March - June)
n = 105
Post-breeding
(July - Oct)
n = 55
WALES
Other
Hymenoptera
Diptera
Grain
Oligochaeta
Coleoptera
Year
n = 277
MEAN (Wales)

One anomaly in the assemblage is the apparent underestimation of ants, which were commonly observed to have been taken in season. Indeed, during the breeding season, ants appear to be a major influence on habitat selection (4.3.3), and yet their remains do not occur in a single faecal sample during that season (Table 5.14). This discrepancy is possibly explained if ants are selected only for feeding to nestlings (5.4, but see 5.3.7). Ant remains appear most frequently during the post-breeding season (36%), and all identified specimens were alates suggesting that predation occurred during swarming on ant mounds before flight. The catching of flying insects by a flock of Choughs has been witnessed in the Isle of Man in September (Batten *et al.* 1973).

It is possible that evidence of earthworms (chaetae and gizzard rings) in faecal residue has been overlooked in the past due to the need for differential examination (5.2.2). The frequency of earthworm evidence across the study region varies considerably, ranging from 6% in the Ramsey Island samples (Table 5.17) collected during the summer to 74% in the winter Cornish material (Table 5.18). The lowest Welsh ($\bar{x}$ 20%) value of 12% at Mwnt-Cemaes contrasts with a high of 31% at Strumble (Table 5.15) - one of the few times that faecal data from these two otherwise similar study areas diverge (*cf.* Diptera, Coleoptera and cereal component variances of only 0-2%). The main variance was found within the winter season, when Cemaes birds took more tipulids.

Figure 5.6 shows the annual diet as represented by the percentage seasonal occurrence of detectable evidence from faecal analysis in Wales. There is close agreement between the Welsh and Cornish winter beetle evidence but the Cornish quotient of earthworms is greatly increased, balanced by less evidence of cereal grain. Choughs are also known to

Table 5.17 Frequency of prey taken by Choughs on Ramsey Island in July 1989 as represented by percentage occurrence of remains in faecal samples; age: A =adult, L =larva

Taxon	% Frequency
OLIGOCHAETA	6
LEPIDOPTERA (L)	2
DIPTERA (L) (all)	29
NEMATOCERA Tipulidae	20
CYCLORRHAPHA Syrphidae	2
Indet.	6
HYMENOPTERA (all)	8
Lasius sp.	2
L. alienus	6
L. flavus	2
Myrmica sp.	4
COLEOPTERA (A, all)	98
CARABIDAE (all)	35
Abax parallelepipedus	4
Amara sp.	10
A. aenea	2
Calathus fuscipes	6
Harpalus sp.	2
Pterostichus sp.	18
P. nigrita	2
indet.	8
STAPHYLINIDAE *Staphlinus ?aenocephalus*	6
ELATERIDAE indet.	2
BYRRHIDAE *Byrrhus* sp.	14
COCCINELLIDAE *Scymnus* sp.	2
SCARABAEIDAE (all)	76
Amphimallon ?solstitialis	76
Cetonia ?aurata	2
CURCULIONIDAE (all)	12
Otiorhynchus ligneus	10
indet.	2
GASTROPODA Helicidae *Trichia striolata*	2
CEREAL GRAIN	4
Total no. samples	49

Table 5.18 Frequency of winter prey at Rame, Cornwall as represented by percentage occurrence of remains in faecal samples and cast pellets; age: indeterminate full-grown except A =adult L =larvae

	% Frequency	
Taxon	Faeces	Pellets
OLIGOCHAETA indet.	74	40
ARACHNIDA indet.	1	0
MYRIAPODA indet.	2	0
DERMAPTERA *Forficula* sp.	6	7
HEMIPTERA	0	7
LEPIDOPTERA (all)	0	20
Indet.	0	13
?*Lasiocampa* sp.	0	7
DIPTERA (all)	14	0
Indet.	2	0
NEMATOCERA (all)	10	0
Tipulidae	8	0
Bibionidae	2	0
CYCLORRHAPHA (all)	2	0
Muscidae *Morellia ?hortorum*	1	0
Scatophagidae *Scatophaga sterorcaria*	1	0
HYMENOPTERA (A, all)	2	13
Indet. ants	2	7
Indet. wasps	0	7
COLEOPTERA (all)	55	80
Indet. (A)	6	0
Indet. (L)	0	7
CARABIDAE (all)	24	53
Amara sp. (A)	5	0
Amara aenea (A)	1	0
Amara aulica (A)	2	0
Pterostichus madidus (A)	2	0
Pterostichus niger (A)	0	13
Pterostichus melanarius (A)	0	7
Trichocellus sp.	0	7
Indet. (A)	16	20
Indet. (L)	1	7
TENEBRIONIDAE (A) *Opatrum sabulosum*	17	20
SCARABAEIDAE/GEOTRUPIDAE (A, all)	25	67
Aphodius sp.	18	7
Aphodius sphacelatus	1	0
Geotrupes sp.	7	7
Geotrupes spiniger	0	60
Oxyomus silvestris	1	0
CURCULIONIDAE (A, all)	1	20
Brachysomus echinatus	1	7
Sitona ?waterhousei	0	13
CEREAL GRAIN/SEEDS	8	7
INDET. FRAGMENTS	1	0
Total no. samples	99	15

consume plant food: oats being a very important component in the Hebrides, occurring in nearly all winter faecal samples of Judy Warnes' 1982 study. This seems to decline southwards for grain, largely barley and wheat (+ occasional other seeds), appeared in 64 Welsh samples (23%), 77% of these being in the winter (Table 5.15): almost 50% of all winter samples contained evidence of cereal feeding. In Cornwall, cereal grain appeared in <10% of the winter Cornish samples (Table 5.18). In addition, one sample from Cornwall included the kernel from a wild or ornamental cherry *Prunus* sp. There is evidence to suggest that cereal and earthworm components are interchangeable as a source of bulk winter protein: in 120 samples with grain/earthworm evidence only 11 contained both, and there was a very strong separation of the two components ($P<0.001$; Table 5.19). Given the general but hidden ubiquity of earthworms, cereal grain, where present, might simply present a 'cheaper' bulk food. Mollusc evidence was infrequent: only a single terrestrial Gastropod (*Discus rotundatus*) and fragments of the common marine mussel *Mytilus edulis*; the latter was possibly a result of Choughs scavenging along cliffs frequented by gulls.

5.3.6 PREY SIZE

In a small captive trial (see Appendix X), the Chough did not respond to prey of <5mm but care must be taken before attributing captive behaviour to wild counterparts since their exposure to varied stimuli is greatly reduced. Proven prey, as revealed by direct observation and especially by faecal evidence, include a number of taxa which are somewhat smaller. With aggregated prey (*e.g.* ants) this size character need not apply, and both *Myrmica* spp. and *Lasius* spp. form an important resource. The Collembola, almost uniformly <5mm in size, are represented by one record, but these soft-bodied animals are unlikely to survive passage through the

Table 5.19 The occurrence of grain and/or earthworms in the Chough's diet. Evidence from all 120 faecal samples collected which contained cereal grain and/or earthworm evidence

	Grain	Earthworms	Grain + earthworms	N
Distribution	59 (49%)	50 (42%)	11 (9%)	120
		$x^2 = 32.55$ d.f.1 $P < 0.001$		

gut in recognisable form. A number of small insects may be the result of casual ingestion whilst working over a range of habitats. The small hydrophilids of the genus *Cercyon* occur both in dung and wet mud, and the related *Helophorus* could also be taken in the latter habitat. Other species, however, seem more likely to be the result of deliberate ingestion. The small ground beetles, *Bembidion lampros* and *Trechus obtusus*, do not exceed 4.5mm, and, whilst the former is both very shiny and fairly active, running about on dry open soils (Lindroth 1973), the latter is dull and less evident in its activity. Similarly, the weevils of the genus *Sitona* are only 3-5mm long but have brightly coloured scales, whilst the smaller *Brachysomus echinatus* (2.2-3.3mm) is both dull and sluggish, and is often found in association with moss on hillsides with short grass (Harde 1984). It seems probable that the bird is capable of responding to prey down to at least 3mm in its natural habitat; Warnes (1982) reached the same conclusion.

5.3.7 PELLET AND FAECES COMPARISON

The absence of cast pellets from Welsh sites (see 5.2.2) raises the possibility that faecal assemblages are not wholly representative of invertebrates ingested. Although the majority of taxa found in pellets in Cornwall are recorded from faeces in Wales, there are some discrepancies (Table 5.18), *e.g.* Lepidoptera (unrecorded in faeces); Diptera (unrecorded in pellets); and Hymenoptera, Scarabaeidae/Geotrupidae and Curculionidae (all under-recorded in faeces). These could at least be partly explained by seasonability in prey selection; it is suggested elsewhere (5.4) that ants are primarily taken as a food for nestlings, and that this accounts for various observational behaviours and the fact that during the breeding season they were not recorded from any of 105 faecal samples. If they are consumed by adults during the breeding season the expected frequency would be as in Cornwall (=2%), where they appeared in 2 of 99 faecal samples but also in 2 of only 15 pellets. The possibility therefore must remain that had pellets been available from Wales, ants might have been found to have featured in the adult diet at that time. On the other hand, ant remains in Cornwall represented winter diet, and the equivalent seasonal value for Wales was greater (=4%, n = 117)(see Figure 5.6).

The remaining exceptions relate either to sporadic incidental prey items, such as *Sitona waterhousei*, a weevil which largely feeds on crucifers, or to the increased precision of identification which is possible with the less fragmented material from pellets, and this should be borne in mind with regard to the hymenopterous component. Some of the differences are also possibly size-related, in that the larger species of ground beetle (*Pterostichus melanarius* and *P. niger*) and the large Dumbledor beetle *Geotrupes spiniger* are more evident in the pellets, although smaller taxa, including lepidopterous larval head capsules also occur. Further experiments with captive birds would help to clarify whether larger prey are significantly under-represented in faecal samples.

5.3.8 A COMPARISON OF CORNISH AND WELSH FAECAL SAMPLES

There appear to be no significant differences in terms of species diversity between the prey items of the Cornish and Welsh Choughs: dividing the number of taxonomic groups represented by the total number of samples in each region gives: Wales .332, and Cornwall .307.

There were differences within taxonomic groups: earthworms were clearly a more important element in the (winter) diet of the two immigrant Cornish birds (74% occurrence in 99 samples), than recorded for Welsh birds (winter = 29%, n = 117), exceeding the frequency occurrence for beetles (*cf.* Tables 5.14 & 5.18). The increased emphasis on earthworms in Cornwall could be explained by the birds' relative inexperience (Meyer 1990, see Appendix IV). It is possible that local edaphic, as well as seasonal factors, also caused some of the differences, although the birds clearly utilise both herbivore dung and sandy grassland in both regions. Indeed, because of the paucity of earthworms in the upper layers of the soil during summer, it is probable that the turning over of dried dungpats provided the Choughs with most of the summer earthworm component; tipulid larvae have also been noted to be similarly aggregated beneath dung (P. Skidmore pers. comm. to P. Buckland). There are, unfortunately, no summer Cornish samples. The dung beetle *Aphodius rufipes* present as larvae, identified by the mandibles, occurs in only two of the Welsh localities, Strumble and Newgale-Solva, and the absence of this apparently eurytopic animal (Landin 1961) from the Cornish material is proably not significant.

5.4 DISCUSSION

The abundance of the commoner invertebrate prey orders was, with the exception of the Oligochaeta, greater in feeding areas than in adjacent unused areas (Figure 5.1); Less usually taken prey was also more abundant in feeding areas, by a ratio of 7:1. Since faecal evidence does not support the hypothesis that ranges are selected for prey diversity (see below), it is likely that Choughs select foraging areas within ranges for prey richness.

Throughout this study, the role of the earthworm has been ambiguous. Barbash (1988) showed that Starling and Rook predation of leatherjackets caused appreciable and significant mortality. It was proposed in Section 5.2.2 that diversity is less important than the availability of key species at certain critical times of the year, and the possibility should be considered that Chough predation of preferential taxa causes localised depletion and affects the results of sampling in the wake of a feeding bout. Direct observation and the pattern of faecal evidence (Table 5.15) give the impression that earthworms are a regular and important prey of Choughs in West Wales. To avoid the problem of sampling locally depleted populations "the usual protocol is to disturb the birds whilst they are feeding and to sample along the search path immediately" (D.B.A.Thompson pers. comm.). However, in this study, an implicit requirement existed not to disturb Choughs, and no such licence, to enable legal disturbance, was therefore sought.

Taken in isolation, earthworm chaetae in faeces will overestimate the importance of earthworms to a greater extent than is likely with evidence from any other prey taxa. In Appendix X it is shown that the chaetae from just one earthworm can appear in at least 12 subsequent faeces. The sampling protocol ensured faecal sampling occurred on separate days in each study area during each visit, thus helping to counteract the problem of overestimation. The additional benefit of occasional direct observations during behavioural observations (Chapter 6), enable it to be stated with reasonable assurance that earthworms were at least a *regular* prey. The possibility also exists that the selection of feeding sites depends on arthropod availability, and that earthworms are taken adventitiously. If earthworms and cereal grain are interchangable as a source of winter protein (Table 5.19), availability of cereal stubble, given its lower collection costs, will reduce earthworm intake. It is also possible that Choughs are preferentially seeking tipulids, which, as subterranean larvae, more closely resemble earthworms than arthropods. The exact role of the earthworm in Chough regional ecology requires further and specific research. Such questions are greatly influenced by the proportions of different habitats available, these are generally determined by farming practices (see Chapter 4).

Apart from earthworms, only earwigs (Dermaptera) were recorded as more numerous away from foraging sites. Faecal evidence (Table 5.14) suggests that earwigs are quite an important Chough food, as they certainly are on Islay, where they were recovered from >66% of 56 Chough pellets (Warnes 1982), and on Bardsey Island (Roberts 1982). Earwigs live on the surface or under stones and old cow-pats, therefore soil-sampling *per se* might under-record their presence. There seems little doubt, judging from faecal evidence (*cf.* Table 5.14), that other taxa, for example weevils (Curculionidae), were also under-represented by choosing soil-sampling in preference to pitfall- or suction-trapping as the primary method of prey investigation. On Islay, no earwig was found in 274 soil samples but 44 were taken from 313 pitfall-traps during the course of a year (Warnes

1982). However, at South Stack, although earwigs were taken by Choughs "consistently at all times of the year", they were not recovered from any of 400 soil samples nor from 240 pitfall-traps (Bullock 1980); a few were found in samples taken at actual feeding sites, as in the present study. This suggests that neither pitfall-traps nor soil-sampling adequately assesses earwig populations, which are surface active in the summer but hibernate below ground in the winter. During this study, randomised sampling within Chough feeding areas helped to overcome the problem insofar as surface elements, such as loose stones etc., would be sampled *pro rata* as frequently as the substrate (see Section 5.2.1).

Previous studies have demonstrated the importance of Coleoptera as a major prey taxon (*eg.* Bullock 1980, Roberts 1982, Warnes 1982), the present study confirms this. Although surface-active ground beetles, such as the Carabidae and Staphylinidae, were under-represented in soil-samples, the use of pitfall-traps would not have wholly redressed the balance (Greenslade 1964, Southwood 1978), since their efficiency is prone to error (Luff 1975), and they catch nocturnal-active taxa. A small experiment was carried out at the end of the study to help clarify the role of pitfall-trapping in Chough food resource studies, and it was found that many of the suitable carabids in Chough feeding areas were nocturnal (Appendix V). From the sampling evidence (Figures 5.2b & 5.3b), beetles were very much more numerous in the two northern study areas: W1/Mwnt-Cemaes and W2/Strumble. Mwnt-Cemaes also had a more diverse invertebrate fauna (Table 5.2) in those feeding sites which were accessible to sampling. Farther south with increasingly intensive agriculture, reduced diversity of Coleoptera is possibly offset by recourse to habitats where prey such as ants, grasshoppers (Orthoptera) and spiders are more abundant, although judged by faecal evidence alone, beetles are as important as in the more agricultural areas (Table 5.15).

Species selection alters: at Newgale-Solva more ground and rove beetles (Staphylinidae) are taken, at Marloes more dung beetles (mainly of the *Aphodius* genus). This latter fact is surprising given the pastoralism at Mwnt-Cemaes and Strumble. It could in part be explained by the reduced sample size at Marloes and a larger proportion of unidentified beetles, including possibly chafers of various species, which were known to occur frequently on the cliffs. The increased emphasis on diptera by Choughs at Mwnt-Cemaes might also have affected the dung beetle intake.

The life-cycles of beetles affect their availability to Choughs. Their frequency in Chough feeding areas/habitats reaches a peak during the months March through June (Table 5.7) but this is not reflected by the frequency of their remains in faecal samples (Table 5.14) - in which the percentage occurrence rises steadily throughout the year from 81% to 95% in the post-breeding period. The frequency of the Carabidae (the most important family) in faeces falls quite sharply during the Chough breeding season; with dung beetles, however, the frequency in feeding areas matches the faecal evidence more closely. The third ranking taxon in faecal sampling was Curculionidae, and yet weevils were never found in live sampling in Wales, although they did occur in the background Cornish sampling (Table 5.8). The faecal evidence of rove beetles, which drops in the breeding season (Table 5.14), also differs from the frequency pattern of abundance (Table 5.7). This might be explained if certain kinds of food (*e.g.* ants) are selected preferentially for nestlings (see below). The bulk of adult diet during the breeding season is dipterous (occurrence 49%), and other coleopterans (scarabaeids (37%) and carabids (30%). Many of the species which compose these taxa are obtainable from cow dung, and this might well represent the 'cheapest' food, appropriate to adults, that is available at this time of year.

Dipterous larvae are a major prey category, as are, to a lesser extent, Crustacea, notably woodlice (Isopoda). These components are fairly evenly distributed within feeding areas across the study range (Table 5.2), a fact confirmed by faecal analysis (Table 5.15). Woodlice are characteristic of maritime crevice communities with a rich loam derived from drift and plant litter (Harding & Sutton 1985). The increased emphasis in northern feeding-sites on diptera larvae (note the high dung-fly (Cyclorrhapha) value at Mwnt-Cemaes and its absence elsewhere), does reflect increased pastoralism. The Nematocera, especially the tipulid, quotient holds up well in soil samples from all areas with the exception of Newgale-Solva, but they are taken more frequently in the northern pastoral areas. It was observed (5.3.3) that the emphasis on Diptera declined markedly after the breeding season despite a continuing availability, and again the dual possibility arises: that Choughs either exploit this resource little after breeding or do so so thoroughly that localised supplies are greatly depleted. The importance of employing a multi-factorial approach and not relying on any one investigation is emphasized since, unfortunately, dipterous evidence does not survive digestion well (5.3.1).

Cereal grain, far less nutritious (see below and Table 5.6), taken from the substrate surface, is an important winter dietary supplement in areas where improved agriculture reduces the availability of pastoral elements (5.3.5 & Table 5.18). Choughs thus adapt their feeding behaviour to both habitat and season, and are able to exploit a wide range of habitat types, usually avoiding intensively improved fields (Warnes 1982), especially in the winter if a shorter day length and reduced invertebrate activity enforces a migration into inland pasture and arable land.

Where soil-sampling under-represents particular taxa, such as earwigs, carabid beetles and some cliff fauna, faecal evidence helps to clarify the position. By having regard to all 'feeding exhibits' (the multifactorial approach mentioned above), a better understanding of the requirements of a species emerges even though comparative analysis is not possible due to differing methodology. For example, the consistency with which weevils and carabids are taken across the Welsh region are better shown by reference to Tables 5.14 & 5.15 than to Table 5.4. A more detailed analysis of seasonality in resource use by Choughs is required, this could involve DNA sequencing to assess elements in the diet not identifiable on faecal fragments (P. Buckland pers. comm.).

Anomalies remain however: the apparent decreased importance of tipulids in the diet during the post-breeding phase (possibly due to harder, drier soils), and the relative scarcity of spider and ant remains in faecal samples despite high seasonal abundance, and, in the case of ants, observed predation (but see Section 5.3.7). Warnes (1982) noted the non-selection of spiders (again with high field abundance) and ants on Islay, and contrasted this with increased usage in Anglesey: a largely heathland area quite different in its physiography (Bullock 1980). Evidence from faecal analysis in West Wales shows a far higher dependence on ants at Newgale-Solva, confirming that the Chough's diet varies with locality (*cf.* Tables 5.2 and 5.10).

Ants highlight this better than any other prey. Cowdy (1973) was the first author to draw attention to their importance in Chough diet, although in 1926, Coombs watched Choughs feeding on ants in Cornwall, and subsequently agreed with Cowdy as to their significance (1978); Holyoak (1967) noted the relationship on the Isle of Man in 1966. Warnes (1982) found ants to be unimportant on Islay, and cites only one observation of ant-feeding; she thought that ants might be uncommon in habitats frequented by Choughs. Bullock (1980) showed that the heathland ant *Leptothorax acervorum* was an important winter food from October right through to the beginning of June. In the precursor to the present study, ants, from both direct observation and faecal evidence, were taken in Cornwall in November and December (Meyer 1990, see Appendix IV); in Wales, ant-feeding was confirmed in November and February (5.4.1). Bullock proposed that different genera of ants were important prey in all 3 of the biotopes within his study: maritime (*Formica*), heathland (*Myrmica* and *Leptothorax*) and farmland (*Lasius*), and that from June to September they were "the most likely prey." Despite this, Owen (1985) concluded that Cowdy was "in error", and that ants were merely "taken seasonally in some areas when the ground is too hard for probing". The evidence from my study does not support Owen's view.

In this study, Choughs were frequently found to be feeding in ant-rich patches which appeared to be fairly localised in that ants were absent from, or much reduced in, nearby areas at the times of highest usage (Figure 5.4). Although based on a small sample, the data (Table 5.7) suggest that Choughs were selecting ant-rich habitats in the breeding and post-breeding seasons while largely ignoring the resource in the winter even though it was present. Various explanations are possible: (i) ant activity is very much reduced in the winter, and there are consequently fewer visual cues to promote hunting, whilst, in the summer, a super-abundance of highly active and visible organisms will trigger feeding; (ii) ants are positively discriminated for as a food for nestlings; and (iii) the cost, in terms of time and effort, of feeding on small-bodied prey at reduced densities is not economical during short winter days (see also Section 5.3.5). Ants are less energy-rich, calories per gramme, than beetles and fly larvae (Table 5.6), although, of course, hymenopteran food can sustain an animal as large as a male Giant anteater, which weighs up to 39kg; such an animal requires 7000 - 14000 large ants per day (Macdonald 1985).

It is possible that ants contain trace elements of value to young Choughs. At Newgale-Solva and Marloes, they dug so vigorously after ants that at times the feeding Choughs disappeared from sight. Birds feeding young must maximize the amount of food obtained within the constraints of maintaining their own condition Richford (1978), and forage so as to maximize return per unit time (Royama 1970). The highest net energy gain (energy gained less the energy required to find and capture it) is achieved by choosing prey with a high nutritive value, large size and/or low handling time (*ibid.*, Zach 1979). If a small prey is locally abundant, the gular pouch may be filled as quickly as when larger, thinly distributed prey are available (Richford 1978).

In general, Choughs were foraging in areas which were generally rich in invertebrates (Figure 5.1), and not on very restricted foci of prey, but obviously this did not always apply. In the case of mound-building ants (*e.g. Lasius* spp.), foci are very easily located, whereupon there is a virtually inexhaustible supply of prey organisms albeit of small body size. Diptera are also frequently to be found in discrete well-defined patches, and these too are often easily located, such as when in cowpats. Larval tipulids are sometimes found congregated beneath cowdung but distribution is generally related to the distribution of host plant communities (Freeman 1967, 1968) and also to vegetation height (den Hollander 1975), in which case they are presumably less easy to find than clumped epigaeal taxa.

The larger-sized earthworms were never found in the soil cores extracted at feeding points (*cf.* Table 5.4), neither were they seen to be taken by the birds. Ruling out the theory that the resource was eaten out, it is suggested that habitats supporting the larger earthworms were not selected, or that the worms were passed over owing to the disproportionate costs involved in extracting and handling them from their deeper burrows (Thompson & Barnard 1984); soil samples, in this study, were 6cm deep. Observations and the results of sampling also suggest that Choughs take the smaller-sized earthworms. No evidence existed to indicate whether Choughs took enchytraeid whiteworms (=potworms), it is thought unlikely due to their small body size relative to length but the possibility cannot be ruled out. In passing, it should perhaps be noted that earthworms have never been recorded as being taken by captive Choughs.

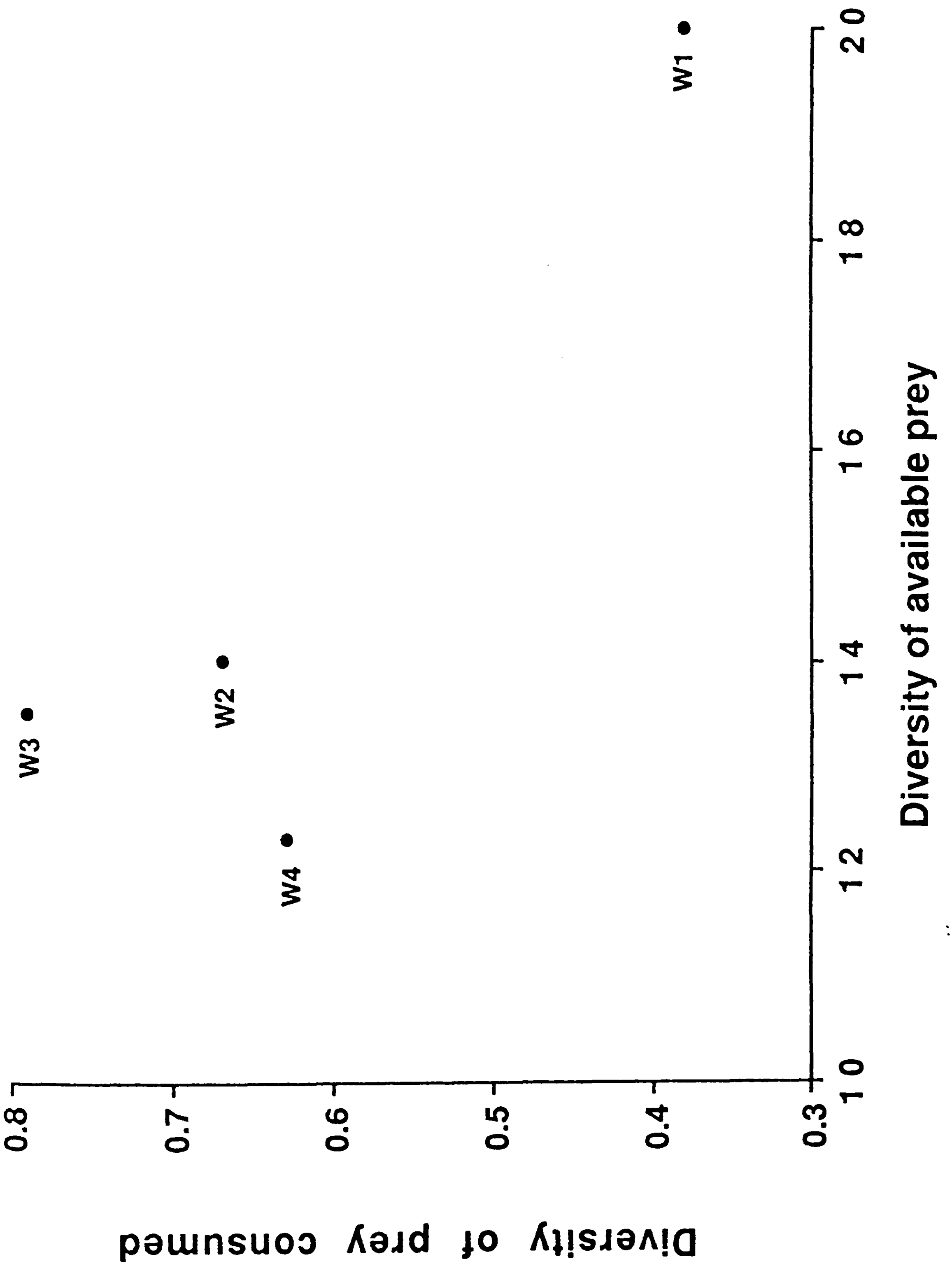
It has already been mentioned that Choughs are able to switch between earthworms and cereal grain as a source of winter protein (Table 5.19). Grain, though, however cheap to obtain, is a poor food for young birds (Morse 1974); this is evinced by the fact that many granivorous birds switch to a protein-rich diet of insects when rearing their young (O'Connor 1984; see also Appendix X). Most invertebrates contain *ca.*50% protein by dry weight (*cf.* only *ca.*15% in grain) (Linton 1927). Richford, who studied Jackdaws on Skomer Island (contiguous with Marloes), argued that when a bird is foraging for its young, time and energy expenditure are best repaid by selecting the most profitable food, therefore the nestling diet is probably the 'best' food available; he found that Jackdaws collected many spiders, principally *Xysticus cristatus* (the commonest thomisid), Hermiptera and Hymenopterous larvae, with perhaps as many as 60+ per sample. House martins select insects with the highest calorific value (Bryant 1973). Carrion crows, rearing newly-hatched young in north-east Scotland, offered a varied diet of small invertebrates, including bees, flies and spiders, but replaced these with tipulid and lepidopterous larvae when the nestlings were older (Yom-Tov 1975). Royama (1966) found that tits regularly punctuated loadings of caterpillars to their young with spiders, despite a higher collection cost and plentiful supplies of caterpillars. Feare (1984) notes the importance of spiders for Starling chicks, and O'Connor (1985) stresses their importance in many nestling diets, suggesting that they might contain trace nutrients lacking in caterpillars and leatherjackets.

The assumption is often made in Britain that the Chough is naturally a coastal species (for example, I suggested above (p.146) that inland migration in winter is "forced"), but elsewhere across its very wide range this is clearly not the case (*cf.* Figure 1.1). Goodwin (1986) proposes that the Chough originated as a montane species and subsequently spread to the cliffs in the west of its range. In north-west Europe, the coast might provide the only satisfactory combination of rocky terrain with caves, fissures etc which is neither covered by vegetation nor snow in the winter; it also remains frost-free, leaving accessible earthbound invertebrates in harsh conditions. Rare sub-zero temperatures in Cornwall (Meyer 1990, see Appendix IV) caused the surviving Chough of a pair to feed exclusively beneath the cover provided by the large rounded and lobed leaves of the Tree mallow, which grew in only one or two discrete zones. Had these not been available, it is possible that the Chough would either have not survived or moved away; Schifferli & Lang (1941) recorded Choughs, with young in the nest, feeding under the cover of woods after an unseasonable snowfall. In mild winters, pasture is apparently preferentially selected (Chapter 4). Why then is this abandoned when the return migration occurs in the early spring? Since invertebrate biomass increases rather than falls off at this time of the year (Wallwork 1976) and since Choughs were not known to travel more than a few hundred metres inland (usually pasture was available near the cliff-top) it is possible that Choughs require: (i) cliff-based prey for their young, (ii) the security afforded by cliffs, and (iii) the opportunity for young birds to develop appropriate behaviours within this, their primary ecological niche. Such development, in an area as complex as habitat recognition, depends on the interaction of genetically controlled behaviour and morphology with learning and experiential feedback (O'Connor 1985). Further evidence of foraging economics suggests also that cliffs are the most profitable habitat *when of high quality* (Chapter 6); thus the migration into pastoral agriculture in the winter might indeed be *forced* if the cliffscape is of sub-optimum quality. It should also be remembered that cliffs could not be sampled as completely as pastoral habitats, and this might have depressed diversity indices.

It follows to ask from this: is the apparent greater diversity of potential prey at the northern pastoral study areas (Table 5.2) 'better' for Choughs than an increased dependence on fewer taxa, if such is indeed the case elsewhere? Despite the absence of detailed information on the abundances of all potential prey, the diversity of actual prey in the diet, as represented by faecal evidence (Table 5.15), does not support the hypothesis that availability of a wider prey spectrum is reflected in the Chough diet: the Mwnt-Cemaes area which shows the greatest potential prey spectrum (D=19.6) has by far the lowest frequency of prey taxa in the faecal collection (0.38), as is summarised in Figure 5.7. The key, in fact, might not be diversity but the availability of certain key taxa at certain different times of the year (Feare 1984). In the case of Choughs in West Wales, this might be summarised thus: cereals/earthworms in the

Figure 5.7

Relationship between the diversity of available potential prey and diversity of prey consumed as shown by faecal analysis



Diversity of prey consumed
0.8
0.7
0.6
0.5
0.4
0.3
Diversity of available prey
10
12
14
16
18
20
W1
W2
W3
W4

autumn/winter; tipulids in the spring; other diptera in the summer; ants in the breeding season/summer; with coleoptera forming a year round resource, its great taxonomic variety ensuring there is usually something 'in season'. As has been shown in Ireland (Bullock 1983b) and Bardsey (Roberts 1982) there is recourse to seashores in the winter in some regions, possibly linked to where there is also an emphasis on machair or sand(dune) feeding (see Roberts 1983). This does not seem to apply in West Wales to any marked extent, there being only two possible sightings during the current study (both at Marloes), and it is possible that seashore feeding is replaced farther south by a movement a little away from the actual shore to the splash and maritime therophyte zones during hard weather periods, as indicated by observations in Cornwall (Appendix IV) and during the current study (Chapter 4).

Finally, I will discuss the background Cornish situation in the light of Chough-derived data from Wales. Figure 5.5 shows the relationship with regard to prey abundance in Welsh feeding areas with that at equivalent Cornish sites. Of the 18 invertebrate taxa most frequently found in Chough feeding areas in Wales, 13 (72%) were found to be more abundant in Cornwall; of the remainder, two were equal. Two of the 3 taxa for which Wales scored more highly than Cornwall are, however, very important: the Nematocera (including the tipulids) and the carabid ground beetles. The Hymenoptera (which includes the ants of course) was one for which no difference was found between the two regions.

It would not be very meaningful to correlate the ranks without correcting for the varying importance of different taxa. Looking at the 10 most frequently found taxa in faecal analysis (from data in Table 5.15), only the Carabidae, Curculionidae and Dermaptera are below tenth rank in invertebrate sampling undertaken at likely feeding sites in Cornwall

(Table 5.8). These are 3 taxa that have already been identified as under-recorded in equivalent Welsh sampling; only the Carabidae scored less in Cornwall than Wales. As an order, the Coleoptera in Cornwall gave a value more than double that for Wales, but Diptera was about 40% greater in Wales than Cornwall (Figure 5.5). The distribution of larval tipulids responds to phytogeography (Freeman 1967), and this highlights an inherent difficulty in speculating the likely feeding sites for birds in areas uninhabited by them at the time; in other words, Choughs will be better at finding food than human imitators. Given this belief and the comparatively invertebrate-rich picture emerging from Cornwall, it is safe to conclude that sufficient food resources probably exist for Choughs provided the habitats which support the invertebrates also exist in sufficient quantities (Chapter 4).

6 FORAGING BEHAVIOUR AND ACTIVITY PATTERNS

6.1 INTRODUCTION

In Chapter 4, the effects on habitat selection of seasonality (possibly linked to breeding constraints) were discussed, *e.g.* the generalised migration from cliffs to arable (late summer) to pasture (winter) and returning to the cliffs in spring. In the preceding chapter (5.4), it was stressed that the highest possible net energy gain (energy gained less the energy required to find and capture it) for birds is achieved by choosing prey with a high nutritive value, large size and/or low handling time; additionally, birds feeding young have to maximize the amount of food obtained within the constraints of maintaining their own condition (Richford 1978). They should, in short, forage so as to maximize return per unit time (Royama 1970). This question of foraging economics is clearly of paramount importance.

In Cornwall, during a precursor to the main study, it was found that the Choughs involved spent the vast majority of their active day in foraging and associated activities (*i.e.* vigilance and moving between foraging areas). The two birds studied were active for >98% of the day, and actively foraged with head down for >60% (Meyer 1990, see Appendix IV). With associated activities included, the amount of time spent foraging accounted for up to 80% of active time. If individuals need to spend such a great proportion of their time searching for food, the maintenance of habitat quality must *ipso facto* be extremely important: any degradation would affect foraging efficiency and, with so little disposable spare time, presumably also their condition and survival prospects.

Even within the limited scope and short duration of the early study, it was possible to demonstrate significant differences in efficiency between the two main biotopes used (agricultural fields and the cliffscape) (*ibid.*). In the main study of foraging behaviour, comparable methods were used to compare efficiency and other behaviours between study areas, which, in turn, could be compared to the Cornish investigation.

The foraging efficiency of Choughs has been examined in the past by measuring the number of pecks and swallows against time or number of paces in different habitats. Bullock (1980) showed that the birds which moved about within habitats most were the least successful foragers, and he was able to relate this to different age-classes of heath and different seasons, establishing that feeding efficiency was highest in burnt heather (30 pecks or 15s per swallow), a fact he attributed to the larger proportion of bare earth (see Section 4.3.3a). It is to be expected that winter utilised habitats (stubble fields etc), because they involve surface-gleaning and bulk intake (a greater proportion of carbohydrates), will be the most productive in terms of quantity per unit time but not neccesarily in terms of energy or protein.

In this chapter, focal-animal sampling is used to investigate activity patterns across the study range in different seasons (6.3.1), and success rates in different habitats (6.3.2). Vigilance behaviour and disturbance caused by other Choughs and by other species, including humans (which affected feeding efficiency) were also investigated, as were the responses of Choughs to disturbance, and consequent minimum flight distances (6.3.3).

6.2 METHODS

The basic methodology is described in Section 2.5.3. Altmann (1973) discussed observational sampling methods, and recommended "focal-animal sampling" in which "all occurrences of specified (inter)actions of an individual ... are recorded during each sample period"; a record is made of the length and the time during which the focal individual is in view. "Once chosen, a focal individual is followed to whatever extent possible..." (*ibid.*). Focal-animal sampling was chosen as a means of providing relatively complete data. The sampling regime involved behaviours being recorded for one minute on every hour and half-hour (one was additionally taken at the first opportunity in case the subject moved out of sight). The exclusive behaviour categories are listed in Table 6.1. Food ingestions were recorded, as were environmental and climatic data. Inter- and intra-specific interactions and their outcomes were recorded as and when they occurred.

Table 6.1 Behaviour categories recorded during focal-animal sampling, with symbols used in subsequent tables

Behaviour	Symbol	Description
Foraging	F	Exclusive feeding, *i.e.* head-down hunting
Vigilance	V	Head-up wariness, scanning for predators etc.
Ground-movement	G-M	Walking translocation: between foraging patches where this did not include 'F'. *Note*: birds so engaged would also be to some extent 'V'
Relocation	ReL	Flighted translocation between foraging areas or sites of other behaviour
Hunting	H	Incorporating all activities integral to F: 'F+V+G-M', does not include 'ReL'
Active	A	Activities *per se*: all behaviours requiring movement: 'H+ReL' or components thereof
Inactive	InA	All static behaviours, *e.g.* resting, loafing, preening. *Note*: also includes periods within roost, shelter or nestsite
Other	O	Any other 'A' behaviour: *e.g.* interactions with other individuals, spiralling flight etc

Analyses were undertaken both for individual study areas and for the *region* (=all study areas combined). Foraging success was assessed by successful peck rate and calculated for different habitats in the range of study areas.

6.3 RESULTS

6.3.1 ACTIVITY PATTERNS

In Wales, 240 focal periods, mainly of *ca*.60s duration ($\bar{x}$ = 61.2s), were recorded (Table 6.2) over 68 days in all seasons. Birds were not marked, and therefore individuals could not normally be identified; the sampling rationale described in Section 2.5.3 helped to reduce bias and focal periods are treated as independent. During the earlier Cornish study, 112 were achieved in addition to 34 longer observations devoted to specific inquiries (Meyer 1990, see Appendix IV). It can be seen from Table 6.2 that the greatest proportion of time (.94) was spent in active behaviour; Choughs at Mwnt-Cemaes and Strumble were almost identical in the amount of time spent hunting. Since data were non-normal and proportional, non-parametric statistics were used: Kruskal-Wallis 1-way ANOVAs were applied to the data sets to determine differences between the 4 main study areas (*i.e.* excluding the Ramsey Island summer inquiry, see Appendix V). Where significant differences were found, the particular pairs of study areas involved were identified by a multiple comparison test (Siegel & Castellan 1988). It was thus shown that Choughs spent significantly less time hunting at Marloes in the south of the study range than at Strumble in the north ($P<0.01$).

The mean time per focal period spent in different activities is given in

Table 6.2 Distribution of focal periods (f.p.) ±1 s.e. between study areas and mean proportions of time (seconds) spent in activity patterns (Act =active, InA =inactive); mean proportion of time spent hunting (*H*), the principal 'Act' component, is also shown

				Mean proportions of time						
Locality	Mean time f.p.	s.e.		Act	s.e.	InA	s.e.	*H*	*s.e.*	N
Wl/Mwnt-Cemaes	62.21	1.53		.95	.02	.05	.02	*.77*	*.04*	82
W2/Strumble	64.55	4.97		.94	.04	.05	.03	*.77*	*.07*	33
W3/Newgale-Solva	58.68	1.32		.95	.03	.05	.03	*.66*	*.08*	31
W4/Marloes	59.80	1.67		.90	.03	.10	.03	*.55*	*.06*	56
WR/Ramsey Island	60.82	1.34		1.0	-	0	-	*.91*	*.02*	38
Region	61.29	0.98		.94	.01	.06	.01	*.73*	*.03*	240
Kruskal-Wallis 1-way ANOVA (excluding WR)			*K*	4.374		6.104		*11.613*		
			P	N.S.		N.S.		*<0.01*		

Pair underlined is significantly different, multiple comparison test P <0.05

Table 6.3, and converted to proportions in Table 6.4. In line with the above findings, Choughs spent more time foraging at Strumble than elsewhere, again very significantly more so than at Marloes ($P<0.01$). This is at the expense of vigilance and time spent in other activities. The north/south dichotomy often appears but, interestingly, the Choughs at Strumble were much less vigilant than those at neighbouring Mwnt-Cemaes ($P<0.001$), where, otherwise, there is usually close agreement. They did, however, spend significantly less time in non-hunting activities than Choughs at Marloes ($P<0.01$). It is certainly possible that the apparently better foraging performance of Choughs at Marloes is a consequence of the larger flock sizes generally seen there. [The Strumble birds unlike those at Marloes, and despite very low numbers being recorded (usually only one pair), successfully bred; although, as pointed out elsewhere (6.4), failure at Marloes was probably due to human disturbance (see also Appendix VIII)].

Table 6.4 also shows that while there was a significant difference in variance between the study areas in ground activity whilst feeding, no significant difference at the 5% level was found between individual study areas; however birds at Strumble were least mobile (as they were least vigilant) at a level very close to 5% significance compared to the other northern area, Mwnt-Cemaes. Neither was there a significant difference between individual study areas in the proportion of time spent flying.

The two southerly, more agriculturally improved, study areas were both 'worked' significantly less intensively than the two northern more pastoral areas (Tables 6.5 and 6.6); additionally, the amount of time spent in plumage maintenance and other non-hunting activities was very significantly greater in the south ($P=0.007$). Analysis of food finding

Table 6.3 Activity patterns, mean time ±1 s.e. per focal period: F =foraging, V =vigilance, G-M =ground-movements (all within hunting bouts); ReL =relocations, *i.e.* flights, O =other; and periods of inactivity (InA), largely resting or loafing; sample sizes as in Table 6.2

	Mean time (seconds)											
Locality	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.
W1/Mwnt-Cemaes	31.7	2.2	13.4	1.0	5.2	1.0	2.8	0.8	6.2	1.5	2.9	1.3
W2/Strumble	42.8	5.9	7.6	1.4	1.3	0.6	8.3	3.4	0.8	0.5	2.9	2.0
W3/Newgale-Solva	28.4	4.0	8.7	1.4	2.1	0.6	4.1	1.4	11.7	3.9	2.6	1.7
W4/Marloes	22.0	3.1	12.2	1.6	2.3	0.6	6.5	2.1	10.6	2.3	7.4	2.2
WR/Ramsey Island	46.3	1.9	8.6	0.8	0.4	0.2	0	-	5.6	1.1	0	-
Region	32.8	1.5	11.0	0.6	2.8	0.4	4.2	0.8	7.1	0.9	3.4	0.8

Table 6.4 Activity patterns: mean proportions of focal period time ±1 s.e. spent foraging (F), vigilant (V), moving on the ground (G-M), in relocation flights (ReL), in other (O) activities and inactive (InA) by study area and region; sample sizes as in Table 6.2

	Mean proportion of time									
Locality	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.
W1/Mwnt-Cemaes	.51	.03	.21	.01	.08	.01	.05	.02	.10	.02
W2/Strumble	.65	.06	.11	.02	.02	.01	.14	.06	.01	.01
W3/Newgale-Solva	.47	.07	.15	.02	.04	.01	.08	.03	.19	.07
W4/Marloes	.37	.05	.21	.03	.04	.01	.12	.04	.16	.03
WR/Ramsey Island	.76	.02	.14	.01	.01	-	0	-	.09	.02
Region	.53	.02	.18	.01	.04	.01	.08	.01	.11	.01
Kruskal-Wallis 1-way ANOVA (excluding WR)										
K	13.872		16.725		9.220		1.758		14.489	
P	<0.01		<0.001		<0.05		N.S.		<0.01	

Column pairs underlined are significantly different, multiple comparison test P <0.05

Table 6.5 Mean proportions of focal period time ±1 s.e. spent active (Act) and inactive (InA) in northern (W1+W2) and southern (W3+W4) study areas; the mean proportion of time spent hunting (*H*), the principal 'Act' component, also shown

	Mean proportion of time						
Season	Act	s.e.	InA	s.e.	*H*	*s.e.*	N
W1+W2 (north)	.95	.02	.05	.02	*.77*	*.04*	115
W3+W4 (south)	.92	.02	.09	.03	*.59*	*.05*	87
z-value	0.89		-1.35		*3.07*		
P	N.S.		N.S.		*0.003*		

Table 6.6 Activity patterns, mean proportions of focal period time ±1 s.e. spent in different activities (F =foraging, V =vigilance, G-M =ground-movements, ReL =relocations, *i.e.* flights, O =other) in northern (W1+W2) and southern (W3+W4) study areas; sample sizes as in Table 6.5

	Mean proportion of time									
Locality	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.
W1+W2 (north)	.55	.03	.18	.01	.06	.01	.08	.02	.07	.02
W3+W4 (south)	.41	.04	.19	.02	.04	.01	.11	.03	.18	.03
z-value	2.82		-0.25		1.78		-0.90		-2.75	
P	0.005		N.S.		N.S.		N.S.		0.007	

rates suggests that not only was feeding less intensive in the south, it was also more successful (6.3.2).

Seasonal breakdowns (winter = November-February, breeding season = March-June, post-breeding season = July-October) for the Welsh region are given in Tables 6.7 - 6.9a-d. Although no significant difference was found between the seasons in the proportions of time spent hunting, even though less time was spent in this activity during the breeding season due to opposing reproductive demands, the proportion of time spent actually foraging (*i.e.* in head-down feeding mode) during the breeding season was significantly less than in the other two seasons (Table 6.8). The greatest proportion of time spent hunting was in the post-breeding season, when the birds were also more vigilant, although not to a significant extent (see Section 6.4). Significantly more time was spent in flight (between foraging patches) during the winter ($P<0.05$), in accord with the observations made during the early Cornish study (see Section 6.4 and Appendix IV).

The mean proportion of time spent hunting in winter in the Welsh region (.74) was exactly the same as that recorded in Cornwall during the earlier (winter) study (Meyer 1990, see Appendix IV). Similar proportions of time were also spent in winter 'head-down' foraging: *i.e.* Wales =.58, Cornwall =.60 (Table 6.8 *cf. ibid.*). Significantly less time was spent in preening and other activities during the winter than at all other times ($P<0.01$); most time was spent in these behaviours during the breeding season ($P<0.01$), with the post-breeding season supporting a central position (Table 6.8 and see Section 6.4).

Sheep and cattle were by far the commonest herbivores on pasture foraged over by Choughs, their presence was noted during 41 (17.1%) and 23 (9.6%)

Table 6.7 Mean proportions of focal period time ±1 s.e. spent active (Act) and inactive (InA) by season within Welsh region; mean proportion of time spent hunting (*H*), the principal 'Act' component, is also shown

	Mean proportion of time						
Season	Act	s.e.	InA	s.e.	*H*	*s.e.*	N
Winter	.98	.01	.02	.01	*.74*	*.07*	38
Breeding	.93	.02	.07	.02	*.68*	*.04*	124
Post-breeding	.96	.02	.05	.02	*.80*	*.04*	78
All	.94	.01	.73	.03	*.06*	*.01*	240
Kruskal-Wallis 1-way ANOVA (excluding WR) *K*	5.556	N.S.	2.211	N.S.	*2.563*	*N.S.*	

Table 6.8 Activity patterns, mean proportions of focal period time ±1 s.e. spent in different activities (F =foraging, V =vigilance, G-M =ground-movements, ReL =relocations *i.e.* flights, O =other) by season within Welsh region; sample sizes as in Table 6.7

	Mean proportion of time									
Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.
Winter	.58	$.06^{a}$	.16	.02	.04	.01	.15	.05	.06	$.03^{a}$
Breeding	.46	$.03^{a,b}$	.17	.01	.07	$.01^{a}$	.08	.02	.14	$.03^{a}$
Post-breeding	.62	$.03^{b}$	.20	.02	.01	0^{a}	.04	.02	.09	$.02^{b}$
All	.53	.02	.18	.01	.04	.01	.08	.01	.11	.01
K-W 1-way ANOVA (excluding WR) *K*	11.995		1.343		24.274		8.839			11.6
P<		0.01	N.S.		0.001			0.05		0.01

Superscript signifies column pairs significantly different, multiple comparison test P<0.05

Table 6.9a-d Activity patterns: mean proportions of focal period time ±1 s.e. spent in various activities (*F =foraging, V =vigilance, G-M =ground-movements*, ReL =relocations *i.e.* flights, O =other) by season in study areas; mean proportion of time spent hunting (*H* =elements of F+V+G-M), the principal activity, is also shown

Table 6.9a Study Area Wl/Mwnt-Cemaes

	Mean proportion of time												
Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	*H*	*s.e.*	N
Winter	.40	.10	.26	.04	.06	.04	.09	.05	.18	.09	*.61*	*.14*	12
Breeding	.50	.04	.20	.02	.09	.02	.06	.02	.08	.03	*.78*	*.05*	54
Post-breeding	.63	.07	.21	.03	.04	.02	0	-	.12	.06	*.87*	*.07*	16
All	.51	.03	.21	.01	.08	.01	.05	.02	.10	.02	*.77*	*.04*	82

Table 6.9b Study Area W2/Strumble

	Mean proportion of time												
Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	*H*	*±s.e.*	N
Winter	.65	.12	.12	.03	.04	.03	.18	.12	.01	.01	*.79*	*.13*	10
Breeding	.68	.08	.11	.03	.02	.01	.16	.08	0	-	*.81*	*.08*	18
Post-breeding	.53	.22	.09	.02	0	-	0	-	.07	.04	*.60*	*.24*	5
All	.65	.06	.11	.02	.02	.01	.02	.01	.01	.01	*.77*	*.07*	33

Table 6.9c Study Area W3/Newgale-Solva

	Mean proportion of time												
Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	.e.	O	s.e.	*H*	*s.e.*	N
Winter	.78	.13	.20	.15	.03	.03	0	-	0	-	*1.0*	*0*	2
Breeding	.42	.08	.14	.03	.05	.01	.09	.04	.25	.08	*.60*	*.09*	24
Post-breeding	.61	.13	.17	.03	.01	.01	.08	.06	.01	.01	*.79*	*.13*	5
All	.47	.07	.15	.02	.04	.01	.08	.03	.19	.07	*.66*	*.08*	31

Table 6.9d Study Area W4/Marloes

	Mean proportion of time												
Season	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	*H*	*s.e.*	N
Winter	.66	.10	.09	.02	.03	.01	.20	.10	0	-	*.77*	*.11*	14
Breeding	.28	.06	.19	.03	.06	.02	.06	.04	.27	.06	*.46*	*.09*	28
Post-breeding	.26	.09	.37	.08	.01	.01	.17	.08	.11	.04	*.50*	*.12*	14
All	.37	.05	.21	.03	.04	.01	.12	.04	.16	.03	*.55*	*.06*	56

focal periods respectively; only 2 focal periods were recorded on pasture grazed by equines (Table 6.10 *cf.* Table 4.5), but horse-grazed fields existed only at Cemaes and Strumble (=*ca*.0.4% of available pasture). Rabbits were patchily distributed, and the effects of their presence not always noticeable during focal sampling (but see Table 4.5 and Chapter 7 for appraisals of their importance). Birds were slightly more mobile on sheep-grazed pasture probably due to the less clumped nature of the dung; this is confirmed by the significantly reduced amount of time spent actually foraging on sheep pasture ($P<0.05$), while no such significance existed in the amount of time spent hunting (Table 6.10).

Foraging performance during time spent in different biotopes was also examined (Table 6.11). Cliffs are by far the most important single biotope in terms of time spent therein (see *e.g.* Figure 4.10) and also in their productivity to Choughs (6.3.2, 6.4); indeed >47% of all focal periods were recorded on the 'vertical' cliffs (excluding contiguous maritime habitats), and yet significantly less time per focal period was spent hunting there than within the old pasture categories ($P<0.001$). This is explained by the fact that cliffs were used more for non-hunting behaviours; for example, Choughs were inactive there for longer periods ($P<0.01$; Table 6.11). Less time was spent in 'head-down' foraging than on unimproved pasture ($P<0.05$). They also moved less on the ground in the cliff environment than elsewhere ($P<0.01$). Vigilance was only marginally affected by habitat; no two affected it significantly although there was a difference in overall variance ($P<0.05$). Stubble was excluded from these analyses because it involves a non-comparable feeding regime. Comparison of the proportion of time spent in flight (=relocation) in different habitats (Table 6.11) is of dubious value because it only accurately records relocation within the same habitat; if the focal bird

Table 6.10 Activity patterns: the mean proportion of time ±1 s.e. spent on land grazed by sheep and cattle in region (F =foraging, V =vigilance, G-M =ground-movements, ReL =relocations *i.e.* flights, O =other); time spent hunting (H =elements of F+V+G-M), the principal activity, also shown

	Mean proportion of time														
Grazer	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.	*H*	*s.e.*	N
Sheep	.51	.04	.21	.02	.09	.02	.11	.04	.07	.03	0	-	*.79*	*.05*	41
Cattle	.66	.05	.22	.03	.04	.02	.03	.02	.04	.03	0	-	*.90*	*.06*	23
Mann-Whitney test															
z	-2.156		-0.070		-1.825		-0.587		-1.025		0		*-1.695*		
P	<0.05		N.S.		N.S.		N.S.		N.S.		N.S.		*N.S.*		

Table 6.11 The effect of habitat type on activity patterns. Mean proportion of focal period time ±1 s.e. H =all hunting time, including elements of F+V+G-M; F =foraging; V =vigilance; G-M =ground-movements; ReL =relocations, *i.e.* flights; O =other

	Mean proportion of time														
Habitat	H	s.e.	F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.	N
Marit. grass/O pstr/ spp-rich/<5cm	.87	.06^{a}	.56	.05^{a}	.23	.02	.10	.03^{a}	.08	.04	.03	.02	0	-	24
Cliff complex	.58	.04^{a,b}	.41	.04^{a}	.17	.02	.04	.01^{a}	.10	.02	.17	.03^{a}	.12	.03	113
Marit. heath	.63	.18	.41	.14	.21	.06	.03	.02	.34	.16	0	-	0	-	8
Marit. heath/burnt	.95	.02	.72	.03	.21	.02	.02	.01	0	-	.05	.02	0	-	14
Marit. scrub	.03	-	0	-	.03	-	0	-	.33	-	.63	-	0	-	1
Evap. hollow/spp-r	.88	.03	.78	.3	.10	.01	0	-	0	-	.12	.03	0	-	24
Ant-rich	.97	.01	.68	.08	.16	.03	.13	.05	.01	.01	.01	.01	0	-	10
Walls	.68	.15	.54	.13	.18	.14	.01	.00	.02	.02	.25	.12	0	-	9
S-Imp. pstr <5cm	.91	.05^{b}	.62	.05	.23	.03	.08	.03	.03	.02	.02	.01^{a}	0	-	24
Imp. pstr <1cm	.67	.33	.60	.30	.08	0	.01	.01	0	-	.31	.31	0	-	3
Stubble	.92	.06	.79	.07	.14	.03	0	-	.08	.06	0	-	0	-	10
All	.73	.03	.53	.02	.18	.01	.04	.01	.08	.01	.11	.01	.06	.01	240
Kruskal-Wallis 1-way ANOVA: main habitats (underlined) *K*	21.720		10.641		10.673		14.787		2.702		19.497		14.695		
P	<0.001		<0.05		<0.05		<0.01		N.S.		<0.001		<0.01		

Superscript denotes column pairs significantly different, multiple comparison test P <0.05 disappeared from sight it was obviously not possible to be sure of its destination: some flights would have been to similar habitats, and some to different ones.

Activity patterns were also examined in relation to various environmental variables, *ie.* temperature, windforce, precipitation and cloud cover (Table 6.12). In these results, due to the large number of comparisons, $P<0.01$ is taken as the appropriate level of significance; levels at *ca.*0.05 may be seen by reference to the table. Choughs spent a greater part of their active time during rainy weather hunting and less in some other activities ($P<0.02$); foraging and vigilance spans within hunting bouts were not significantly affected by any of the climatic variables measured, although warm weather increased the proportion of time spent foraging. Choughs were slightly more mobile, both on the ground and in the air, during cold weather ($P<0.02$), but significantly more likely to fly during very cloudy or overcast conditions ($P=0.002$). It has already been shown that 'other activities', *e.g.* plumage maintenance, sunning etc., occur very largely within the cliff environment (Table 6.11, $P<0.001$); as might be expected, warm weather seemed to affect these behaviours (Table 6.12), while rain, to some extent ($P=0.013$), decreased them. Indeed, the greatest climatic effect was caused by cloud cover, or the lack of it, on such behaviours: heavy cloud cover very significantly decreased the amount of time spent in behaviours other than hunting ($P<0.001$), and it might also have increased the amount of time spent inactive, though not significantly at the 1% level (Table 6.12). Wind less than Beaufort force 7 did not significantly affect the amount of time spent hunting or in secondary behaviours, although in strong winds they chose to feed in sheltered sites, as demonstrated by Bullock (1980), and strong wind also impaired foraging *success* (6.3.2). Very little Chough activity, during focal sampling, was recorded in winds stronger

Table 6.12 The effect of extremes of various climatic variables on activity patterns in region over all habitats; the mean proportion of focal period time ±1 s.e. spent hunting (H =elements of F+V+G-M), the principal activity, is also shown

Variable		F	s.e.	V	s.e.	G-M	s.e.	ReL	s.e.	O	s.e.	InA	s.e.	*H*	*s.e.*	N
Temperature <11°		.46	.05	.16	.02	.07	.02	.13	.03	.12	.03	.06	.02	*.65*	*.06*	61
Temperature >15°		.59	.03	.17	.01	.03	.01	.05	.02	.10	.02	.05	.02	*.78*	*.03*	97
Mann-Whitney test	*z*	-1.940		-1.060		-2.517		-2.422		-1.970		-1.099		*-0.364*		
	P	0.052		N.S.		0.012*		0.015*		0.049*		N.S.		*N.S.*		
Windforce <2		.61	.03	.17	.01	.04	.01	.06	.02	.09	.02	.01	.01	*.81*	*.03*	118
Windforce >5		.56	.08	.22	.05	.03	.02	.05	.04	.09	.05	.06	.06	*.75*	*.09*	18
Mann-Whitney test	*z*	-0.267		-0.145		-0.621		-0.601		-1.421		-0.492		*-0.526*		
	P	N.S.		N.S.		N.S.		N.S.		N.S.		N.S.		*N.S.*		
No precipitation		.52	.02	.17	.01	.04	.01	.08	.01	.12	.02	.06	.01	*.71*	*.03*	213
Precipitation		.60	.07	.24	.04	.07	.02	.09	.07	.01	.01	0	-	*.90*	*.07*	14
Mann-Whitney test	*z*	-0.298		-1.768		-1.827		-0.107		-2.478		-1.260		*-2.371*		
	P	N.S.		0.077		0.067		N.S.		0.013*		N.S.		0.018*		
Cloud cover <1/4		.57	.03	.16	.01	.04	.01	.05	.02	.16	.03	.03	.01	*.74*	*.04*	103
Cloud cover >3/4		.50	.04	.18	.02	.05	.01	.09	.02	.06	.02	.11	.03	*.70*	*.05*	65
Mann-Whitney test	*z*	-1.060		-0.135		-1.783		-3.096		-3.856		-1.923		*-.407*		
	P	N.S.		N.S.		0.075		0.002**		<0.001***		0.055		*N.S.*		

than force 5 or 6: in fact, only one period each at forces 7 and 8. During gales and severe weather, Choughs remained in regular shelters in both the Welsh and Cornish phases of the study.

6.3.2 FORAGING SUCCESS

Feeding success, as measured by rate of successful pecks (seconds per swallow), during 'head-down' foraging and over all hunting time, is shown in Table 6.13. During actual foraging, ANOVA shows a significant difference between the study areas, although not between any individual couple. The data suggest that feeding was not only less intensive in the two southern areas (6.3.1), it was also more successful: items were found >3s faster when foraging, and >4s faster over all hunting time (Table 6.14), but the data do not take into account nutrititive return per item (see Section 5.3).

Success in different habitats is given in Table 6.15. The success rate is predictably increased during surface-gleaning on stubble-fields and where birds are feeding on clumped prey (*e.g.* at anthills), otherwise there is no significant difference in success rate between the habitats most frequently used, nor is there any significant difference between the cliff region and semi-natural zone (Table 6.16). Since it concerns future discussion, however, it should be noted that during foraging prey was found nearly 1s more frequently within the cliff complex than in the second most successful habitat (excluding ant-rich), short semi-improved pasture, and >1s faster over all hunting time. The mean success rate during which was 1 swallow per 17.2 seconds (1/17.2s), the winter rate on cliffs and semi-natural habitat was 1/13.2s, and the mean rate during

Table 6.13 Mean swallowing rate (seconds/swallow) ±1 s.e. during head-down feeding time (=foraging 'F') and all hunting time (H) in study areas and combined (=region) in focal periods

	Mean rate during				
Locality	F	s.e.	H	s.e.	N
W1/Mwnt-Cemaes	10.19	1.76	14.93	2.51	71
W2/Strumble	15.98	4.02	21.44	5.26	18
W3/Newgale-Solva	8.06	2.30	13.37	3.79	21
W4/Marloes	8.37	2.75	11.13	3.37	36
WR/Ramsey Island	23.07	3.16	27.46	3.80	38
All (=region)	12.82	1.24	17.23	1.61	184
Region excluding WR	10.15	1.25	14.57	1.70	146
Kruskal-Wallis 1-way ANOVA *K*	7.823	*P* <0.05	6.215	N.S.	

Table 6.14 Mean swallowing rate (seconds/swallow) ±1 s.e. during foraging time (F) and over all hunting time (H) in northern (W1+W2) and southern (W3+W4) study areas, excluding Ramsey Island

	Mean rate during				
Locality	F	s.e.	H	s.e.	N
W1+W2 (north)	11.36	1.63	16.25	2.27	89
W3+W4 (south)	8.25	1.92	11.95	2.53	57
t-value	1.23	N.S.	1.26	N.S.	

Table 6.15 Mean swallowing rate (seconds/swallow) ±1 s.e. in focal periods during foraging time (F) and over all hunting time (H) in different habitats in Welsh region

	Mean rate during				
Habitat	F	s.e.	H	s.e.	N
Maritime grass - old pasture/ spp-rich/<5cm	12.56	3.25	19.05	5.05	23
Cliff complex	9.88	2.08	13.51	2.65	68
Maritime heath	13.25	4.93	25.75	9.11	4
Maritime heath/burnt	19.24	6.09	24.80	7.73	14
Maritime scrub	0	-	0	-	1
Evaporated hollow/spp-rich	25.31	3.56	29.02	4.09	24
Ant-rich habitats	6.51	2.60	13.03	6.24	10
Walls	14.89	8.47	18.39	10.54	7
Semi-improved pasture <5cm	10.85	2.37	15.09	3.18	23
Improved pasture <1cm	17.67	-	20.00	-	1
Stubble (surface grain-feeding)	3.49	0.76	4.64	1.16	9
All	12.82	1.24	17.23	1.61	184
Kruskal-Wallis 1-way ANOVA between principal habitats (underlined) *K*	1.654	N.S.	1.469	N.S.	

Table 6.16 Mean swallowing rate (seconds/swallow) ±1 s.e. in focal periods during foraging time (F) and over all hunting time (H) in main biomes (excluding stubble-feeding)

	Mean rate during				
Biome	F	s.e.	H	s.e.	N
Clifflands	13.66	1.58	18.19	2.00	130
Semi-natural	12.13	2.22	16.93	3.09	44
Mann-Whitney *z*-value	0.242	N.S.	0.098	N.S.	

winter over all Wales was 1/10.8s; seasonality did not significantly affect foraging success (Table 6.17). The effects of climate extremes on foraging success are given in Table 6.18. In contrast to its lack of effect on the actual proportion of time spent feeding (4.3.1), strong wind significantly reduced foraging success (P=0.02; see Section 6.4).

Although the success rate was better on cattle-grazed pasture, Mann-Whitney U-tests revealed no significant differences between sheep-grazed and cattle-grazed pasture over either actual feeding time (cattle = 1/8.9s, sheep = 1/11.7s; Z=-.3717, n = 58) or generalised hunting time (cattle = 1/11.9s, sheep = 1/17.5s; Z=-.4218, n = 58).

6.3.3 INTERSPECIFIC INTERACTIONS

All visible interactions with other species were recorded as and when they occurred. Table 6.19 shows the causes of disturbance to Choughs at different times of the year and for all year. Human disturbance (excluding observer pursuit disturbance), though not agonistic, is clearly the most frequent, accounting for more than 40% of all incidents and increasing during the summer. Only the Raven caused frequent disturbance throughout the year; although this was matched in the breeding season by the Carrion crow, this species was not a serious problem at other times. Early in the breeding season (March/April), however, Carrion crows represented the most serious disturbing influence for they made direct attacks straight at feeding Choughs, even, on occasions, low-level 'hedge-hopping' approaches from some 200 metres distance. The only other disturbing influence recorded at a frequency of >10% was aircraft activity during the summer.

Table 6.17 Mean swallowing rate (seconds/swallow) ±1 s.e. in all habitats, and natural cliff and semi-natural habitats during foraging time (F) and over all hunting time (H) in focal periods

	Mean rate in									
	All habitats during					Natural & semi-natural during				
Season	F	s.e.	H	s.e.	N	F	s.e.	H	s.e.	N
Winter	10.84	3.50	14.18	4.48	23	13.24	4.61	17.25	5.90	17
Breeding	10.19	1.45	15.54	2.11	90	10.10	1.46	15.49	2.13	89
Post-breeding	16.79	2.34	20.37	2.83	71	17.42	2.41	21.14	2.92	68
Year	12.82	1.24	17.23	1.61	184	13.27	1.30	17.87	1.68	174
Kruskal-Wallis 1-way ANOVA *K*	0.829	N.S.	0.405	N.S.		1.175	N.S.	0.429	N.S.	

Table 6.18 The effects of climate on foraging success in Welsh region. Mean swallowing rate (seconds/swallow) ±1 s.e. during foraging time (F) and over all hunting time (H) in focal periods

		Mean rate during				
Variable		F	s.e.	H	s.e.	N
Temperature <11°		8.04	2.07	12.03	3.01	40
Temperature >15°		15.04	1.93	18.94	2.38	81
Mann-Whitney test	*z*	-1.698		-1.538		
	P	0.0895		N.S.		
Windforce <2		14.60	1.72	18.82	2.17	99
Windforce >5		6.15	5.01	7.53	5.89	12
Mann-Whitney test	*z*	-2.321		-2.142		
	P	0.0203*		0.0322*		
No precipitation		13.60	1.38	18.21	1.78	160
Precipitation		8.28	2.72	12.23	3.90	13
Mann-Whitney test	*z*	-0.914		-0.793		
	P	N.S.		N.S.		
Cloud cover <1/4		16.24	1.97	21.03	2.49	80
Cloud cover >3/4		11.26	2.58	15.45	3.39	40
Mann-Whitney test	*z*	-1.780		-1.642		
	P	0.0750		N.S.		

Table 6.19 The causes of disturbance towards Choughs in different seasons (W =winter, B =breeding season, P-B =post-breeding season)

	Percentage interactions			
Initiater	W	B	P-B	All
Human	28.6	47.2	50.0	41.2
Raven	33.3	12.4	13.3	19.8
Carrion crow	1.6	13.5	3.3	7.7
Helicopters/aeroplanes	1.6	5.6	13.3	5.5
Peregrine falcon	6.3	5.6	0	4.9
Extrinsic noise (*eg.* gunshot)	4.8	4.5	3.3	4.4
Jackdaw	3.2	5.6	0	3.8
Starling	7.9	0	0	2.7
Fox	3.2	0	6.7	2.2
Rook	3.2	1.1	0	1.6
Buzzard	0	0	6.7	1.1
Thrush	3.2	1.1	0	1.1
Dog (unaccompanied)	1.6	0	3.3	1.1
Windblown debris	1.6	1.1	0	1.1
Unknown	0	2.2	0	1.1
Magpie	0	1.1	0	0.5
Interactions (N)	63	89	30	182

Table 6.20 Approximate flight distances at which Choughs respond to disturbance in different seasons (W =winter, B =breeding season, P-B =post-breeding season)

	Percentage occurrences			
Flight variable (m)	W	B	P-B	All
<10	49.0	37.5	23.5	40.2
10-25	7.8	20.3	23.5	17.4
25-49	9.8	17.2	23.5	15.9
50-99	29.4	15.6	11.8	20.5
>100	2.0	7.8	5.9	6.1
Occurrences (N)	51	64	17	132

Most serious disturbances to feeding Choughs occur at flight distances of <10 metres (Table 6.20); this increases through the year as birds become concentrated on nest sites or dependent young. Potential danger is usually noticed at 50-100m when evasive action is taken. Virtually all flights from a distance of <10m were as a result of surprise encounters. On >36% of occasions the Choughs resettled nearby (Table 6.21), and usually continued feeding within 12 minutes, often after a period of vigilance and/or preening on a nearby vantage point, usually a fence post. On a greater number of occasions (45% of those timed, and 54% of all records), Choughs departed from the immediate vicinity; a slight increase during the breeding season was the result of birds' visiting their nest-site. Of disturbances specifically attributed and numbering ≥10, those occasioned by Carrion crows and humans caused the greatest disturbance in that they caused the Choughs to leave areas altogether (on 58% & 57% of occasions respectively). Of disturbances caused by aeroplanes and helicopters, 30% occasioned the Choughs to leave a feeding area, while of 27 caused by Ravens, only 22% resulted in the Choughs' departure. Table 6.22 shows the different responses caused by the main initiators: after only 3% of those caused by humans did the Choughs resume feeding immediately, compared to a third of all those attributed to Ravens. Of all initiators, Carrion crows caused the most serious response and, over and above the 58% complete departures from feeding areas, not once did the Choughs begin feeding again immediately (n=12). Peregrines caused only 6 recorded disturbances.

If agonistic interactions are separated out from all others, the Raven accounted for nearly half all records and the Carrion crow for exactly half and the Peregrine for nearly 10% (Table 6.23). In the winter, only the Raven and Peregrine caused disturbance, while in the breeding season,

Table 6.21 Responses by Choughs to disturbance in different seasons (W =winter, B =breeding season, P-B =post-breeding season)

	Percentage responses			
Response	W	B	P-B	All
Depart from area	46.9	58.8	48.0	54.4
Resettle	10.9	12.5	4.0	10.7
Settle nearby out of sight	9.4	10.0	4.0	8.9
Resettle same site	9.4	5.0	16.0	8.3
Settle on vantage point - vigilant or preen	7.8	5.0	12.0	7.1
Scramble, circle in flight	7.8	5.0	4.0	5.9
Some resettle/some depart	4.7	1.3	0	2.4
Evade and continue	3.1	2.5	0	2.4
Responses (N)	64	80	25	169

Table 6.22 Frequency distribution of mean time elapses before recommencement of feeding by Choughs following disturbance by various causes in different seasons. Time categories: A =immediate; B =2-12mins; C =departed area; D =vigilant then C; E =flock separated, part=A/part=C (total n = 147)

	No. within span/season																			
	Winter					Breeding					Post-breeding					All				
Initiater	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Human	0	5	10	1	0	2	15	15	4	0	0	4	4	0	0	2	24	29	5	0
Raven	6	4	2	0	1	1	7	1	0	0	2	0	3	0	0	9	11	6	0	1
Carrion crow	0	2	0	0	0	0	1	7	0	2	0	0	0	1	0	0	3	7	0	2
Aircraft	0	0	1	0	0	1	0	2	0	0	1	5	0	0	0	2	5	3	0	0
Peregrine	0	0	2	0	0	0	4	0	0	0	0	0	0	0	0	0	4	2	0	0
Starling	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0
Jackdaw	0	2	1	0	0	0	2	1	0	0	0	0	0	0	0	0	4	2	0	0
Extrinsic noise	0	0	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0	5	0	0
Rook	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	2	0	1	0	1
Fox	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1
Buzzard	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0
Raptor sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Other	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0
Unknown	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	2	0	0
All	12	14	23	1	3	4	30	30	4	2	5	10	8	1	1	21	54	61	5	6

Table 6.23 Agonistic interactions towards Choughs in different seasons (W =winter, B =breeding season, P-B =post-breeding season)

	Percentage interactions			
Initiater	W	B	P-B	All
Raven	80.0	27.3	50.0	47.7
Carrion crow	0	45.5	16.7	25.0
Peregrine falcon	20.0	4.5	0	9.1
Buzzard	0	0	33.3	4.5
Rook	0	4.5	0	2.3
Magpie	0	4.5	0	2.3
Interactions (N)	15	22	6	44

Table 6.24 Agonistic interactions by Choughs in different seasons (W =winter, B =breeding season, P-B =post-breeding season)

	Percentage interactions			
Receiver	W	B	P-B	All
Raven	0	52.2	20.0	44.8
Jackdaw	100.0	30.4	0	27.6
Buzzard	0	13.1	20.0	13.8
Rock dove	0	0	40.0	6.9
Magpie	0	0	20.0	3.4
Interactions (N)	1	23	5	29

the Carrion crow emerged as the most formidable threat with the Raven in second place, and the Peregrine scoring only the same as the Rook and Magpie, although, of course, its attention was potentially more serious.

The Chough itself harried the Raven more during the breeding season than *vice versa*: >50% of 23 recorded instances of Choughs attacking other species; over the year as a whole, the Chough gave the Raven almost 'as good as it got' (45:48%) (Table 6.24)! The Jackdaw received >1/4 of all attacks (these were generally deterrents from feeding in close association) and the Buzzard nearly 14 percent.

6.4 DISCUSSION

Choughs spend at least 90% of their time active, about 75% hunting for food, and approximately half all daylight time actually in 'head-down' foraging mode. The study area where Choughs spent least time feeding was Marloes, at the southern edge of the study range (Tables 6.2 & 6.4). In this area, previously considered to be less well favoured for Choughs due to its more improved agriculture, not only did the Choughs spend less time feeding, their success rate was also better than farther north in apparently more suitable pastoral country (Tables 6.13 & 6.14). The reason for this could be due to availability of preferential habitat and the *quality* of the clifflands. The cliffs to the north of Pembrokeshire trend to a north-westerly aspect and receive less solar radiation, less wind exposure and reduced oceanicity; the slopes tend to be more scrubby, unless actively managed as on the Cemaes Head reserve. On slopes with a south-westerly aspect, there is more short/open vegetation, which not only gives improved access to food but allows greater insolation, which of itself actually promotes invertebrate activity, *e.g.* ants. The Marloes peninsula (Figure 2.9, and see Appendix VIII) illustrates this well: the northern side with predominantly scrub vegetation was never seen to be used by the Choughs, whilst the southern side was in continual use, and, as stated above, with considerable foraging success.

Results presented in Chapter 4 (*cf*. Figure 4.7) show the increased amount of time spent on the cliffs of the Marloes peninsula: about 75%, compared to less than 40% at Mwnt-Cemaes. Cliffs rendered of a high quality by environmental forces might be preferentially selected by Choughs in favour of contiguous traditional pastoralism, and, therefore, compensate for unsuitable agriculture even to the extent of over-riding its state altogether. There is little doubt though that without sufficient high-quality natural cliffscape, some management is probably essential to enable Choughs to maximise their potential in any particular area. Mixed grazing of cliffslopes can, by the reduction of sward height, creation of open areas, and input of organic material, only be beneficial.

Table 6.11 shows that, whilst on the cliffs, Choughs spend significantly less time active than when on adjoining (semi-)natural pasture, and more time there in other behaviours. Reference to Table 6.15, however, reveals that foraging success is somewhat better than in grassland, so it would be unwise to associate reduced activity in a particular habitat as an indication that it is less suitable. The discussion on ant-feeding (4.3.5) perhaps illuminates this. The 'north/upland/pastoral' and 'south/lowland/improved' dichotomy (Tables 6.5, 6.6 & 6.14) appeared to be a convenient way of demonstrating the benefits of pastoralism but in fact the results were inconclusive: in some tests no significant difference was found between the two categories; in others, however, there were surprising differences, *i.e.* significantly less time was spent hunting in the south but foraging success was greater there.

Comparison of activity patterns within separate study areas (Tables 6.9a-d), suggests that winter foraging in the southern areas is as time-consuming, or more so, as in the north (mean proportion hunting time Marloes =.77 *cf.* Mwnt-Cemaes =.61); in contrast, summer foraging at Marloes occupied only .48 of daytime, compared to .83 at Mwnt-Cemaes. One of the reasons, of course, depressing the summer values of time spent hunting and foraging are other demands associated with breeding and rearing young (*e.g.* incubation and brooding) but this is a fairly constant demand across all areas irrespective of habitat quality except where this might be so different as to affect reproductive success.

Choughs spend more time hunting in the post-breeding season than in any other; this is perhaps surprising when one considers the demands of provisioning altricial young. However, it was found that Choughs feeding nestlings make great use of clumped food, especially ants. Since Choughs throughout the year spend about three-quarters of their active time hunting, it seems that recourse to densely clumped food reserves, such as ants, on account of the nutritional benefits discussed below and the cost benefits, is of crucial importance during the nestling period. It was also shown, due largely no doubt to the demands of incubation, that Choughs spent significantly more time engaged in non-hunting activities during the breeding season ($P<0.01$). Therefore, during the post-breeding season, parent Choughs will need to replenish their energy reserves.

More time will need to be spent feeding during the post-breeding season because changes, as a result of breeding constraints, in habitat-use and, therefore, diet (5.3.3) do not significantly affect foraging success (Table 6.17). The rate is somewhat faster during the breeding season, when an increased number of smaller items, such as ants, are collected quickly to present to the young in the form of a bolus. A slowing of the intake rate, by as much 42%, during the post-breeding season could be due to juvenile care, a constraint on selecting optimum habitats because of such care, or to seasonal and climatic effects on food supply and accessibility (*e.g.* dry, hard ground). Only during the breeding season does the success rate in natural and semi-natural habitats (10.1s/ swallow) exceed the mean for all others (12.8s; Table 6.17), suggesting that cliffs during the early summer are the most invertebrate-productive habitat; indeed, ant-rich habitat was the most productive of all (excluding cereal-stubble). Very often such habitat was to be found on the cliffslopes, but mainly during this study the two were considered separately; if combined, ant-rich habitat would increase still further the cliff success rate (*cf.* Table 6.15). It was shown in Figure 5.4 that Choughs made considerable use of ant-rich habitats during the breeding season and immediately afterwards.

That time spent foraging decreases during the breeding season, and rises to a peak immediately afterwards (Table 6.8), but that success increases during the breeding season (Table 6.16), reflects the parents' need to feed their young, and confirms that a modification of dietary behaviour will influence the selection of habitat (see Section 5.4). Were this not so, it might be expected that Choughs would select habitats which offered similar returns to those selected at other times of the year. The Choughs were considerably less mobile yet more vigilant in the post-breeding season, both on the ground and in the air (Table 6.8) presumably due to the constraints imposed by caring for less mobile juveniles and possibly because they were present in small groups. Still (1989) found that young Choughs tend to be found in smaller flocks. However, she concurred with Dunnet *et al.* (1969) that young corvids move around more, possibly to avoid competition; however, while this may be true of young birds feeding independently, flocks of any size greater than family units were very rare in my study areas, and, consequently, almost no intraspecific conflicts were recorded throughout the entire study. Increased mobility in the winter suggests either that it is necessary in order to visit a range of habitats or that breeding constraints discourage mobility.

Vigilance did not seem to be affected by the patchiness of food resources (Table 6.10) but if the increase noted in translocations both on the ground and in the air (which include vigilance but to a degree which was impossible to measure accurately without sophisticated video recording equipment) are taken into account, vigilance associated with feeding on sheep-grazed pasture and dung would be expected to increase in line with that noted by Still (1989). However, she proposed that patchy food increased vigilance because it represented definable resources which were worth defending from members of the same species. If this had been the case during the present study, the proportion of time spent vigilant *while feeding* would be expected to be greater but, as noted above, no intraspecific agonistic behaviour was recorded, and so it is reasonable to assume that the usual pattern of vigilance decreasing with increasing flock size (Pulliam 1973) is countered if very small flock sizes remove the need to defend resources.

Pulliam (*ibid*), Caraco (1982), Pulliam *et al.* (1982), Hart & Lendrem (1984) and Lima (1987) all state that vigilance scans are instantaneous and unpredictable. Lendrem *et al.* (1986) stated that this was to prevent predators being able to forecast the inter-scan interval and thus make a final uncovered hunting approach. Data gathered during the course of this study, together with equivalent data from other workers has shown by spectral analysis of series that there are non-random fluctuations in the magnitude of scans and intervals (Desportes *et al.* 1991, see Appendix IX).

The reduced mobility of Choughs on the ground within the cliff environment (Table 6.11) is probably a reflection of their preference for this habitat for such activities as sunning, sheltering and preening. The post-breeding season, as represented by the amount of time Choughs seem to have at their disposal for such behaviours (Table 6.8), occupies a midway position: possibly where opposing demands reach a peak. Sample sizes are small for some seasons in some areas, and this might explain some of the low levels of agreement seen in Tables 6.9a-d; local conditions are also likely to have important effects.

Bullock (1980) showed that Choughs are influenced in their choice of feeding sites by wind direction and velocity; it was not possible in the present study to gain comparable data (due to the extensive nature of the project) but it was shown that a wind strength of less than force 5 did not significantly affect the activity budget (Table 6.12). However, in force 5 or 6 on the Beaufort scale, slightly less time was spent feeding and slightly more time visually vigilant (the calls of other birds on several occasions caused Choughs to abandon feeding, and in conditions with a high wind-noise factor these would be harder to hear); more time was also spent in other activities such as sheltering, resting and preening.

Evans (1976) has reviewed the effects of wind on foraging shorebirds, and buffeting is known to be a problem for long-legged species like the Redshank (Speakman 1984). The noise factor of windy conditions, depending on how important the sense of hearing is to hunting Choughs (do they use the vibrations set up by worms for example?, see also Section 1.3.1), might also explain the decreased feeding success given in Table 6.18. Strong winds might impair hunting efficiency, and buffeting affect the ability of the birds to balance, but is difficult to see how it could affect subterranean prey invertebrates. No other climatic variable appeared to affect foraging efficiency within the Welsh region. That a lack of cloud cover, rather than temperature, very greatly increased the amount of time spent in non-hunting activities, probably only merits the conclusion that sunny conditions are indeed utilised *a priori* for activities which are not possible at other times, such as sunning!

Unfortunately, no summer evidence exists for Choughs in Cornwall, however evidence presented in Chapter 5 shows that invertebrate abundance and diversity is greater in Cornwall than Wales, and this could accordingly be expected to enhance foraging success there proportionally. The success rate achieved in Cornwall during the earlier short-term study (Meyer 1990, Appendix IV) was better but the two studies are not directly comparable since the main habitat used in Cornwall was a dung-rich stubble-turnip field, the equivalent of which in Wales was only found at Mwnt-Cemaes, and at a location farther from the coast, which would have decreased its usage.

Human encroachment into Chough habitat occurs mainly during the summer (June-August), spanning the breeding and post-breeding phases of the Chough's life cycle: >30% of all recorded disturbances were by humans at that time (Table 6.19). Many Chough nests are placed well away from casual human reach, and these are seldom disturbed during the critical breeding phase (March-June). Where a traditional nest-site is situated at a human 'honey-pot' area such as occurred at the north end of the Mwnt-Cemaes study area (at the end of a footpath *cul-de-sac*), and at Marloes, breeding success can be affected: both these nests failed to produce young in 1988. At Marloes, steps were taken to reroute a path thus creating a buffer zone of about 100m radius round the clifftop above the nest, an area the Choughs often frequented. This diversion might have been instrumental in the success of the site in 1989 (2.3.2). As can be seen from Table 6.20, a buffer zone of 100m radius around nest-sites should be sufficient to provide the necessary security.

As the summer progressed, human disturbance fell off from 42 to 15 occurrences (there were 18 winter disturbances); however it is when young birds have left the nest and yet are much in evidence nearby - calling, following their parents, and reluctant to fly - that disturbance from walkers, picnickers and curious sightseers can be most troublesome. At this time minimum flight distances increase: during the winter almost half of all flights were occasioned from a distance of <10m. This dropped by >75% during the post-breeding season; in other words, the birds were less tolerant of disturbance.

No other source with the possible exception of the Raven in the winter, and the Carrion crow during the breeding season caused serious disturbance. During the post-breeding phase (Table 6.21), Choughs were more likely to resettle in the same site or nearby on a prominent perch than at other times of the year, again this was apparently due to the presence of juveniles, however, by far the most frequent response to disturbance at all times was to quit the area altogether; this is more likely following human and Carrion crow disturbance than after that initiated by Ravens (Table 6.22). Gunshots, even when distant, always caused evacuation from an area, unlike aircraft noise, which, on 7 out of 10 occasions, merely interrupted feeding. Irrespective of cause and season, Choughs left feeding areas on *ca*. 45% of occasions and remained in >50%. Otherwise, the flock separated: individual birds doing one or the other. In the breeding season, the ratio was 50:50. No human disturbance was intentionally agonistic, the only species to cause actual physical threat were the Raven, Carrion crow and Peregrine (Table 6.23).

It has been shown that Magpies can be very seriously affected by agonistic Carrion crows (Baeyens 1981); the Magpie was the only other corvid frequently seen feeding, usually in pairs, near Choughs, *e.g.* in the same field, in both Wales and Cornwall during this study. Lovari (1981) advanced the theory that *Pyrrhocorax* was phylogenetically related to *Pica* and *Cyanopica* as well as *Corvus*. Magpies employ various methods of avoiding Carrion crow attacks, and Rowley (1973) and Roell (1978) noted that flocks of a usually subordinate species (in these cases, Magpies and Jackdaws) would sometimes 'swamp' the aggressor and deter territorial aggression. Baeyens (*ibid.*) quotes an instance of reversed dominance, in which Magpies chased away Carrion crows, in much the same way as Choughs during this study were occasionally seen to chase Ravens away; he also suggests that the Magpie's ability to resist Carrion crow attacks is influenced by habitat.

The theory that Jackdaws were a principal reason for the Chough's decline in some areas is not supported by the results in Table 6.24, which shows that all serious interactions with Jackdaws were instigated by Choughs. Some depletion of food resources is possible but the respective diets of the two species are not broadly comparable (1.3.1); Darke (1971) saw a possibility of competition when the two species were rearing young in close proximity. No disturbance by domestic livestock was witnessed. At one site (Marloes), Starlings appeared to cause disturbance during the winter by their extremely close association with Choughs, at which times the Starlings seemed to be using them as cues to locate food.

7 RE-ESTABLISHMENT OF THE CHOUGH IN CORNWALL WITH REFERENCE TO ITS CONSERVATION IN WEST WALES

7.1 INTRODUCTION

The Royal Entomological Society (RES) (1986) after liaison with a wide range of agencies including the Nature Conservancy Council (NCC), National Trust, IUCN and Forestry Commission published a 'Code of Conservation Practice' on re-establishment with wider applications than entomology. It holds that "The use of re-introductions and re-establishment of animals and plants... is widely accepted as constructive for the conservation of the countryside". A view echoed by the NCC (1985) in their Corporate Plan 1986-1991. It is also though seen as a measure of last resort, with risks of undesirable side-effects, and inferior to translocation (Garson 1990).

As stated in Chapter 1, a primary aim of this project was to examine the feasibility of re-establishing[1] the Chough in Cornwall: this is a long-held desire of the Cornish people, of many amateur and professional naturalists in the south-west of England, and of others with interests in that part of the world, including H.R.H. Prince Charles - the Duke of Cornwall - who was an early supporter of the project. The link between Cornwall and the Chough is long-established, a fact evinced by the vernacular 'Cornish Chough' in many old bird books (3.2), and its position surmounting the Duchy's insignia (Figure 7.1). The Chough died out as a breeding species in Cornwall in the 1940s (3.3.1). Extinction in

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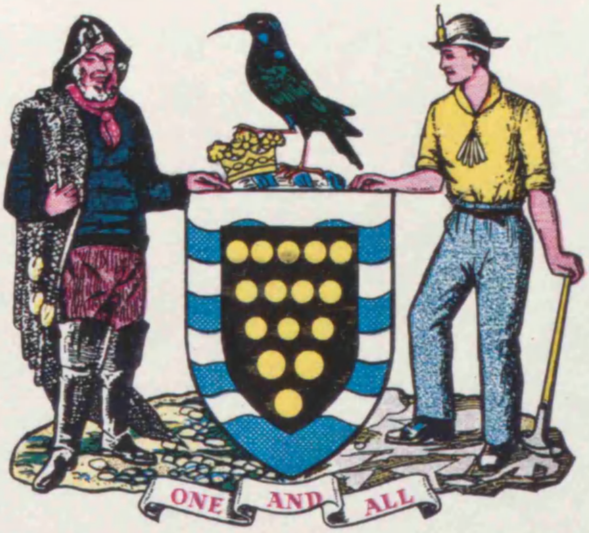
[1] 're-establish' is used in preference to 're-introduce' because it concerns a species in an area of former occupation (after the RES (1986) guidelines).

CORNWALL COUNTY COUNCIL



Description

Sable fifteen bezants in pile within a Bordure barry wavy of eight Argent and Azure and over the crest on a wreath Argent and Azure a Chough proper resting the dexter claw upon a ducal coronet Or; on the dexter side a fisherman holding over the exterior shoulder a net, and on the sinister side a miner resting the exterior hand on a sledge hammer all proper.

Figure 7.1

The Cornwall county shield

Cornwall also meant extinction in England, after a former distribution from Kent along the southern English coast around Land's End to north Devon (3.3). Recolonisation in Cornwall would assume wider implications insofar as it would provide for a more continuously distributed series of populations from Brittany along the coast of Wales to the Inner Hebrides (Table 1.2).

Given, therefore, and leaving aside for the moment the desires of local people, that the Chough as a species is: (i) scheduled as endangered within Britain; (ii) protected throughout Britain and the EEC; (iii) indigenous Cornish fauna of recent lineage; (iv) agriculturally benign; and (v) a 'flagship' species indicative of high quality natural and semi-natural habitats and low-intensity agricultural systems (Bignal & Curtis 1989), it is difficult to see the concept of re-establishment as contentious. [This is of course provided that the habitat can support a viable population.] However, the same can probably not be said for the methods that might be employed to attain this end (7.2).

In the wake of accelerating local extinctions across the world, the re-establishment of animal species as part of a conservation strategy is increasingly seen as a valid adjunct to conservation (NCC 1985). One of the first and most successful attempts has been with restoring the Arabian oryx in Oman, a project still underway which began in the early 1960s (Grimwood 1963, 1964). The first captive-bred oryx (17 in all) did not arrive in Oman until 1980 (Fitter 1982); six years later a net population increase of 10-15% per annum was forecast (Stanley Price 1986). This author believes that technically the Arabian oryx can make the necessary physical, physiological, behavioural and social changes needed to lead an independent existence in its native habitat, but notes that the attainment of independence may take a long time. Captive held representatives of species are very often the only available material with which to work; Martin (1975) reviewed many such examples in conservation.

With specific reference to birds, Halliday (1978), Mountfort (1978) and Gooders (1983) reviewed some recent attempts that have involved reintroductive elements. Birds-of-prey have often been the subject: these have ranged from the assisted natural recolonisation of the Osprey, recounted by Brown & Waterston (1962) and 'on television every year' (Gooders 1983) to recent attempts to return the Red kite to northern England, which the popular press has again avidly followed. After considerable expenditure in time, effort and resources, the White-tailed sea eagle is becoming established on Rhum off the west coast of Scotland (Love 1983); the same species has been the subject of an intensive project in Germany, recounted in great detail by Fentzloff (1984). On account of the passions they provoke, birds-of-prey are by no means the best subjects for such projects, but they do tend to be the ones that secure the high level of funding required. Re-establishment schemes are inherently expensive (Brambell 1977): the Arabian oryx project is costing millions of dollars, while the Cornell University Peregrine project was in the mid-1970's costing about $700 per release bird (Temple 1977). When not birds-of-prey or mammals which are considered beautiful, subjects are often otherwise large and showy, *viz* the Great bustard in southern England (Collar & Goriup 1980). Such attributes can work against successful recolonisation, for they attract public interest and consequent disturbance. Large individuals and their social organisations require large tracts of territory, and of course birds-of-prey are still regularly killed by many gamekeepers, certain farmers and shooters.

Slightly down the scale of public recognition, waterfowl and pheasants also attract wealthy devotees, and have provided subjects within the *local extinction/captive breeding/re-establishment* scenario (see, *e.g.* Kear 1975, Ridley 1986). The Nene or Hawaiian Goose story is well-known but somewhat chequered (Kear & Berger 1980, Devick 1982, Stone *et al.* 1983): after an auspicious beginning, during which numbers increased from *ca*.600 in the early 1970s to *ca*.925 in 1975, the population declined by about 50%, due to low reproductive success, mortality from introduced predators, and poor nutrition and relatively poor weather in the highland areas where the species became confined. A recovery plan was formulated in 1983 by the U.S. Fish & Wildlife Service which included a predator control programme, research into nutritional requirements, release sites at lower altitudes, and the recommendation that captive breeding continue to bolster the wild population.

Pheasants appear, on the surface, ideal *captive breeding/re-establishment* subjects: they are adaptable, and prolific breeders with a long captive history. Matt Ridley of the World Pheasant Association (WPA), in an unpublished document (*Re-introducing pheasants to the wild*) in the mid-80s, saw the Cheer pheasant as a prime candidate for re-establishment. The project began in 1978 in the Margalla Hills National Park, Islamabad, Pakistan, after the species died out there in 1976 (Hussain 1986). The chosen site was a fully protected area of apparently ideal country: steep, grassy slopes typical of the middle ranges of the Himalayas (Lelliot 1981, Garson 1983). Between 1978 and 1985 nearly 2000 eggs were despatched to Pakistan from WPA sources in the U.K. but <15% survived to 6 weeks (Ridley 1986). As with the Nene, the plan had to be rethought; even those poults which did leave the open-topped rearing pens were not surviving. The main problems were poorly developed predator avoidance behaviours and habitat deficiencies (Garson *et al.* 1991). Once rearing techniques were refined, such as by reducing human contact with young birds and rearing with actual or surrogate Cheer parents, survivability improved and breeding in the wild has been attempted. However, great problems with habitat suitability remain. As with the Chough, the Cheer pheasant has evolved in close association with human land management practices, and depends very much [illegible] on such for its future (*ibid.*).

The RES (1986) code, referred to above, states that "re-establishment for conservation may be species-orientated or site-orientated." As a rather extreme example of the latter, Anderson (1986) recounts a case study of restoring an entire National Park in Africa. The Cornish 'Operation Chough' project has elements of both and is compatible with the NCC's Corporate Plan 1986-1991, which said: "Creative conservation seeks to enlarge the resource of nature by reintroducing species which have been lost"; such schemes "are an important means of replacing some of the past losses of wildlife". The plan also mentions the importance of "local initiatives". The NCCS is responsible for the Scottish sea eagle project.

Guidelines that reflect scientific opinion on release programmes were drawn up in 1960-70s mainly under the auspices of the International Union for the Conservation of Nature and Natural Resources (IUCN) (see, *e.g.* Anon 1967, 1987) and the then World Wildlife Fund (WWF) (Boitani 1976). The U.K. Committee for International Nature Conservation set up a working group on introductions, which reported in 1979. The recommendations of this report have been adopted by both the NCC and the Royal Society for the Protection of Birds (RSPB) as a set of criteria to test the suitability of proposed release programmes. These criteria are summarised in Table 7.1.

Table 7.1 Criteria for re-establishment of locally extinct species

1 There should be good historical evidence of former natural occurrence

2 There should be clear understanding of why the species was lost to the area. In general, only those lost through human agency and unlikely to recolonise naturally should be regarded as suitable candidates for re-establishments

3 The factors causing an extinction should have been rectified

4 There should be suitable habitats of sufficient extent (of sufficient quality) to which species can be brought

5 The individual organisms taken for such attempts should be from a population as close as possible to that of the native population

6 Their loss should not prejudice the survival of the population from which they are taken

With regard to the Chough, criterion #1 is not in dispute (see Chapter 3), and #2 was also discussed in that chapter: the Chough is a sedentary species and therefore unlikely to recolonise naturally (Coombs 1978). Criteria #3 and # 4 are addressed, in part at least, by this project. Criteria #5 and #6 would not apply if captive-bred founder stock were used (see below).

To summarise (if it is agreed that the concept is sound): before re-establishment of the Chough in Cornwall is seriously considered in any material way, the causes behind the original disappearance and the feasibility of successful recolonisation have to be understood as well as possible. These issues are examined in this chapter, which has been published in a reduced form in Meyer (1989a).

7.2 METHODS OF ASSESSING FEASIBILITY

The feasibility of returning the Chough to Cornwall depends on 4 main provisos: (1) understanding as fully as possible the reasons for its original decline; (2) investigating whether Cornwall is able to support the species today; (3) if so, investigating how a viable wild population could be re-established; and (4) assessment and, if appropriate, implementation of a re-establishment programme. These provisos are closely related to the general criteria given in Table 7.1.

The first of these provisos was analysed and discussed in Chapter 3; the results are summarised in Section 7.3.1. No. 2 has formed an important part of this project, and was addressed by analysis of the background habitat and invertebrate spectra in Cornwall, and by their comparison to those used currently by Choughs in West Wales, and is further discussed in Section 7.3.2. The third proviso is the equivalent of Criterion 4 in Table 7.1, and depends on biological and practical considerations; these are outlined in Section 7.3.4. Proviso #4 will rely on decisions taken by other interested parties and agencies based upon the results of this project and those of other workers, and is discussed in Section 7.4.

7.3 SUMMARY RESULTS

7.3.1 THE DECLINE

Darke (1971) and more recently Owen (1985) have discussed some of the factors involved in the decline of the Cornish Chough; for a full review see Section 3.4. The factors believed to be largely responsible are both direct and indirect. Among the direct effects are disturbance caused by physical human presence (*cf.* 6.3.3), hunting, egg-collecting, trade in live birds. The indirect effects presented by increasing human pressure, particularly the changes in habitat brought about by agricultural change have obviously been important (3.4.6e); these embrace the decline of tin mining, changes in the pattern of crofting, the reduction of grazing pressures and the consequent scrubbing-over of previously grazed cliff regions, the ploughing up of natural and semi-natural habitats, especially heathland (Mitchley 1990), increasing intensification, application of chemicals and biocides (see also Appendix III), the development of tourism and the opening up of the countryside by road and rail arteries (fuelling the increasing physical presence mentioned above), and the destruction of Choughs in gin traps set for rabbits. Disease might have played a part in the decline but it is unlikely to have been a primary cause (3.4.4). There is little evidence of any interspecific competition or heavy predation pressure (3.1, 3.4.5 & 6.3.3).

Data presented in Section 4.5 showed that habitat differences which existed between Wales and Cornwall in the mid-C19 have virtually disappeared (see Sections 4.6 & 7.3.2).

7.3.2 THE HABITAT AND PREY BASE

Results of behavioural studies of feeding Choughs in Wales indicate that quality of prime cliff habitat is of more importance than the extent of various sub-optimum habitats (6.3.2 & 6.4). Breeding records were of little value in assessing the relative performance of the study areas owing to inadequate annual data. The impression gained during the course of this study is that successful breeding of the currently very thinly distributed population is governed more by extrinsic factors (*e.g.* human disturbance) than deficiencies of habitat quality *per se*. High juvenile survival has been shown in other corvids, *i.e.* Jackdaws, Rooks, Carrion crows and Ravens (Holyoak 1971) in contrast to the Great tit (Bulmer & Perrins 1973) and various other species (Lack 1946, 1954).

On the basis of foraging economics, Chough habitat to the south of the Welsh region, even though agriculture is more intensive and the quality available habitat reduced to a narrow coastal zone, is more productive of invertebrate prey than northern 'upland' pastoral farmland and scrubby cliffs. However, despite an inferior cliffscape, the invertebrate *diversity* in Chough feeding areas, was greatest at Mwnt-Cemaes (Table 5.2), as was the frequency with which beetles (the major prey taxon) were found at actual feeding sites (Table 5.4); at Strumble (the other northern site) beetles were found only slightly less frequently. This apparent contradiction is partly explained by the fact that while behavioural observations were possible on clifflands, invertebrate sampling very often was not, and this will have caused under-representation of cliff habitats. Invertebrate diversity in Cornwall is discussed below.

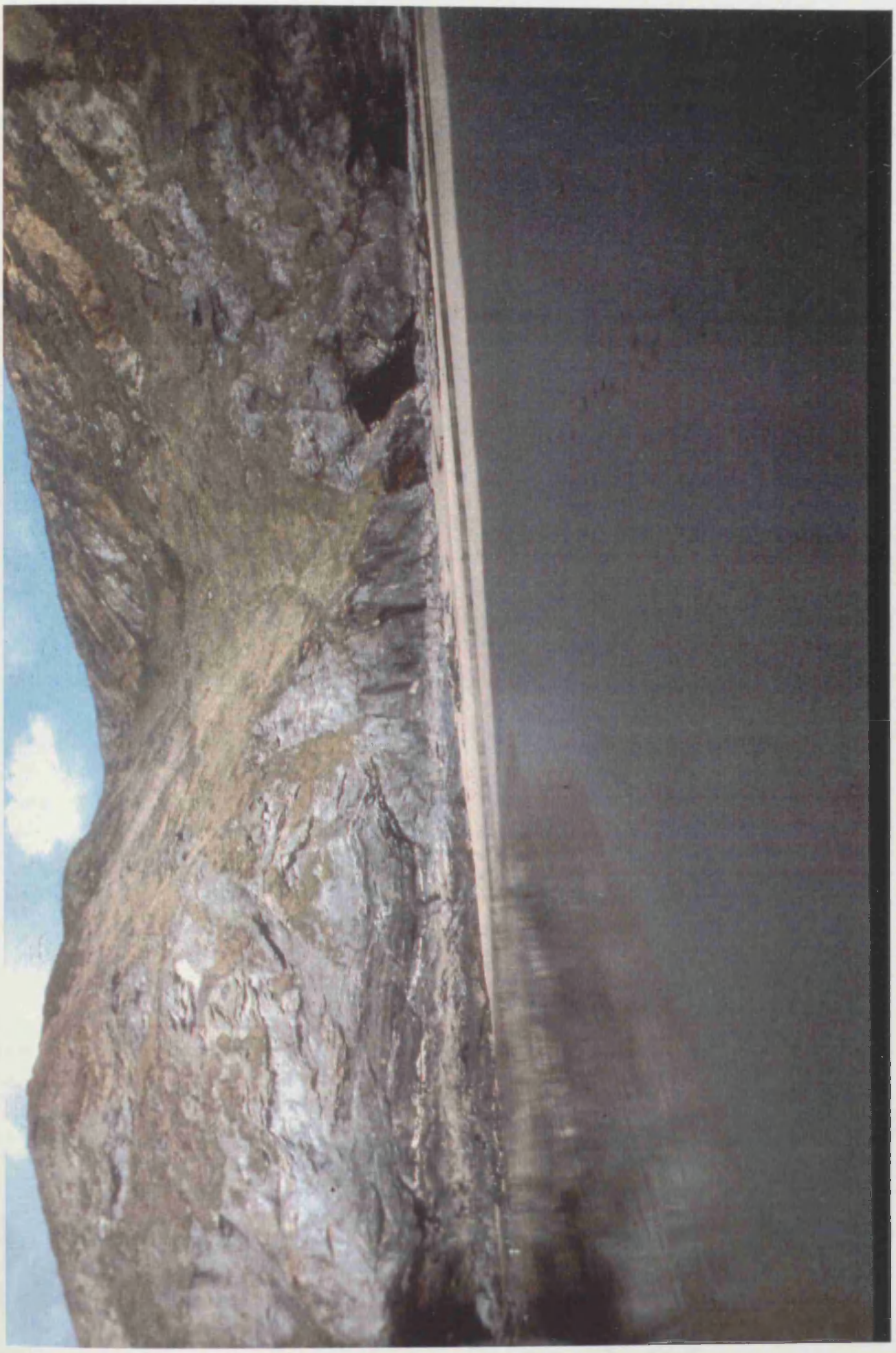
Optimum conditions for Choughs would have the dual advantages of: (i) good quality clifflands, including slopes with sparse vegetation (maintained by exposure, geology, and/or high grazing levels) and a range of aspects to the southern hemisphere, in order to capitalise on the effects of exposure (west to south) and morning insolation (east to south) promoting invertebrate activity; and (ii) an abutting pastoral low-intensive agriculture from which livestock has access to the cliff region.

It was noticeable that one small patch of suitable cliffslope at Cemaes Head, maintained at an optimum level more by a mosaic of rock and shallow soil than exposure, was exhaustively used by Choughs at all times of the year. Similarly, on a narrow promontory, Dinas Fawr, near Solva (Figure 2.8), the south-facing side, rich in invertebrates, particularly ants (see Chapter 5), was frequently used by Choughs while the opposite side, sheltered from prevailing winds, was heavily scrubbed and never seen to be used for feeding even though it supported a successful nest site; where the coastline turned northwards from Dinas Fawr, and yielded a westerly aspect, it was again intensively used. A similar situation applied at Marloes (see Section 2.3.2, Figure 2.10). Usage by Choughs of the study areas is explained in Appendix VIII.

Against this could be argued that Choughs survived longest in Cornwall on the north-facing coast (Figure 3.2). It is possible that *generalised* coastal aspect is secondary to the pattern of radial decline shown in Figures 3.3 and 3.4. The site of the last breeding Choughs in Cornwall appears, even several years after their departure, very suitable (Figure 7.2). This impression was further enhanced by botanically-based investigations (4.4.2). Even a generalised north-westerly facing coastline, if indented, accommodates a range of aspects including south-

Figure 7.2

Beacon Cove, the home of the last Choughs in Cornwall



westerly ones, *viz* Cemaes and Strumble Heads (Figures 2.6c & 2.7). If quality of habitat is more important than extent, it is quite possible that coves and promontories on a north-west facing coast will provide pockets of habitat as suitable as might be found on greater reaches of south-west facing coast. Promontories are, of course, the next best thing to entire islands, which accommodate the greatest length of coastline (necessarily of all aspects) relative to land mass. With the added benefits of mainland herbivore access, and sympathetic surrounding agriculture, optimality will be increased still further.

One important difference, historically, between Cornwall and all other regions of the British distribution is the absence of substantial off-shore islands. When human persecution was a serious threat to Chough viability in Cornwall, the presence of islands, such as exist in Brittany (certainly responsible for the continued existence of Breton Choughs (A. Thomas pers. comm.)) and in all other parts of their recent and current British range, would have provided invaluable sanctuaries; a view supported by Rolfe (1966). The islands of Ramsey, Skomer and Bardsey in Wales are all important recruitment centres. The Calf off south-west Isle of Man safeguarded Manx Choughs when indiscriminate shooting in the C19 almost totally wiped it out (Cullen 1989). Rathlin off N Ireland, and Islay, which supports most of the Scottish population, are further examples of the strategic importance of islands as population centres.

There is no record that the Isles of Scilly, though in many ways an ideal location, have ever supported a resident population. They are possibly too distant, at 45km off the south-west of Cornwall, to be a mainland recruitment centre, and there are no other islands of sufficient size closer inshore. Lundy Island, midway between the English south-west peninsula and south Wales in the Bristol Channel, would probably have been a staging post between the two regions, as well as supporting its own small population until this died out due to human activity at the end of the C19 (Owen 1985). Darke (1971) reports one bird staying for there 10 days in 1952. Two Choughs, which appeared fortuitously at the beginning of the project in east Cornwall, in an area close to the city of Plymouth with no previous record of Chough occupancy, appeared to experience no day-to-day survival difficulties until one was affected by Gapeworm *Syngamus trachea* infection (see Section 3.4.4 and Appendices IV & VII). The remaining bird departed about 3 weeks later (7.5).

When invertebrate diversity in Cornwall was compared to that in Wales (5.3.4), it was found to be considerably richer, perhaps responding to a north>south cline in invertebrate biomass (see also Chapter 8). Research in Wales was directed largely by current Chough usage while that in Cornwall could not be, save that the areas surveyed were all historically important for Choughs (2.3.3). Actual sampling sites in Cornwall were selected on the basis of morphological similarity with used sites in Wales, and as the Welsh trips were followed immediately by equivalent Cornish work, in all other respects at least, the research was comparable. Any bias that existed in Wales regarding under-sampling of precarious cliff sites would have been replicated in Cornwall.

The accessible sites chosen as having a high potential feeding quality in Cornwall all had diversity indices (D) >20.0. Those appearing slightly less favourable for Choughs (equivalent to the Welsh 'control' sites) ranged from D 6.7 to 12.9, more diverse than all the Welsh sites except Mwnt-Cemaes, which was unique insofar as it was a reserve long managed for its Chough population (P. Taylor pers. comm.). Even so, its diversity within prime feeding sites was slightly less than that of the 'worst'

Cornish site: the Lizard (*D*=19.6 *cf.* *D*=20.4).

The key prey taxa were also all more abundant in Cornwall, with the exception of the Nematocera and Carabidae (see Figure 5.5 and Section 5.4 (p.154)). Earthworms in Cornwall were the only taxon with a regional Availability Index (*AI*) >1.0; but without more work the significance of this cannot be evaluated. Hymenopteran values were virtually identical between the two regions, perhaps vindicating the selection of sites in Cornwall. Since it would be wholly against accepted Erringtonian law (3.4.5a) to suggest that the invertebrate prey base in Wales is permanently reduced by Chough activity, it may be concluded that the invertebrate prey base in Cornwall is either more diverse or, more likely, that a broader sampling programme would reduce the regional disparity.

Analysis of faecal evidence (5.3.5) provides incontrovertible proof of prey selection and helps to validate invertebrate sampling. In this way, the true value of Dermaptera (present in 8% of 277 faecal samples) is probably more accurately revealed. Unfortunately no pellets were available from the Welsh population. Their availability would have reduced latent bias in the assemblages even though a comparison from the early Cornish investigation (5.3.7) showed that many of the taxa found in the pellet range were also represented in the faecal assemblage; the exceptions being Lepidoptera and certain beetle species, notably Curculionidae and Geotrupidae. No dipterous evidence was found in the Rame pellet assemblage. Additionally, most of the taxa represented in the Cornish pellets were found in Welsh faeces (Table 5.18). Nevertheless, the collection of pellets from Wales would have been valuable in helping to validate the faecal evidence, in particular, low hymenopteran values; there was, however, considerable evidence to indicate that ants are selected preferentially for feeding to nestlings, and that this accounts for their relative scarcity in adult faeces. It was not possible to examine directly chick diet for the same reason as it was not possible to collect pellets, *i.e.* nest and roost sites were inaccessible.

Notwithstanding these shortcomings, some useful information was achieved by the Welsh faecal evidence, which, with direct evidence from specific feeding sites, confirmed that the important invertebrate prey taxa for Choughs in Wales were Oligochaeta, Diptera, Hymenoptera and Coleoptera. Cereal grain formed the bulk of the vegetable intake, taken mainly in late summer, autumn and early winter (Figure 5.6). This highlights the seasonality of Chough behaviour. Where the agriculture allows, Choughs tend to move into pastoral systems during the winter; a little to the north, Owen (1985) found the same pattern of behaviour. An examination of comparative foraging success (Chapter 6), however, suggests that this is accounted for by sub-optimum cliffs, possibly due to geology or encroachment by scrub where exposure and/or grazing pressures are low.

The quality of habitat in Cornwall is assessed as being analogous to that used by Choughs in Wales. There is some evidence to show that grazing pressures, other than on conventionally improved monocultures, are generally less in Cornwall. Bullock (1985) considered the coastal pasture at Predannack, the sampled area during the present study, to be "borderline" for Choughs. In coastal parishes, the differences are not great but sheep numbers are significantly less in Cornwall ($P<0.01$; see Section 4.6.2): in fact less than half the Welsh number; this is partly redressed by a significantly greater ($P<0,05$) population of cattle. The resource of cow-dung provides a potential year-round source of invertebrate fauna, even during adverse weather conditions. Dung can be probed, broken open or turned over depending upon its condition, and it also creates favourable conditions for soil invertebrates, such as tipulids, in the aureole beneath. Recourse to cattle-grazed vegetation (even improved *Lolium* ryegrass swards) is probably an essential element to year-round Chough viability if the cliffscape is anything less than optimum. It would, though, be possible to substitute horses and ponies for cattle, since the important dung fauna, such as scatophagid flies, the scarabaeid *Aphodius rufipes* and tipulid larvae, and are not usually dung specific (R. Crowson pers. comm., Ritcher 1958, Landin 1961).

Populations are usually restricted by social factors or by the resource in shortest supply (Watson 1973), and so this aspect of Cornwall's suitability might be crucial: is such a shortfall identifiable in *key* areas, and if so, how revertible is it? In order to understand this and form a sensible answer, the exact physical area of any re-establishment attempt must be clearly defined so that management effort can be concentrated where it will be most effective. This is, of course, precisely what is happening in areas of Britain which currently support Choughs and where conservation interests have influence. Such a convergence illustrates an important aspect of this study, and the benefits which can accrue from separate yet allied projects. It is probably reasonable to argue that if such management is possible in areas of current distribution, then there is no reason why similar management should not be exerted on corresponding sections of coast elsewhere. It is the focus of attention that is the critical exercise. An accurate identification therefore of proposed 'functional units' (see Section 4.1) in Cornwall (within a continuum or extended complex) is important, and should extend beyond the narrow limits allowed by this initial study.

On the other hand, it is surely possible to prevaricate endlessly. Re-establishment of locally extinct fauna or flora is not an exact science. One of the key benefits of the Lizard is its strategic position and the concerted conservation interest within the region. Whether or not there are more suitable localities than the Predannack cliff region is a matter for discussion. On the basis of my own experience coupled to that of Ian Bullock, the western coast of the Lizard, including the Point itself, provides the best opportunity due to its extensive rugged and exposed coastline of proven historic significance, central position and tradition of rough grazing.

With increasing awareness and affluence, the problem of persecution in Cornwall should today be averted, indeed, it is reasonable to expect that the Cornish would guard jealously their national emblem were it to return once more as a breeding species. The above-mentioned lack of off-shore islands in Cornwall to act as Chough refuges, sanctuaries and recruitment centres could to some extent be turned into an advantage if the Lizard and West Penwith peninsulas were to be regarded as quasi-islands and the *problems* associated with human presence removed (7.4).

With regard to this idea, the concept of island biogeography and the use of habitat islands as nature reserves is discussed by Diamond (1975), May (1975), Diamond & May (1976), and Simberloff & Abele (1976). Although there would undoubtedly be problems of human encroachment, it is difficult to see wild terrestrial predators posing a significant problem to a species such as the Chough. Problems of reduced genetic diversity, often appearing in isolated island communities, would be reduced or removed altogether if a continuum of such sites could be established, effectively 'linking' Brittany in the south with Wales in the north.

As a footnote, the behavioural deficiencies of captive bred birds when released into the wild should not be overlooked. Dowell (1990a,b) demonstrated the vulnerability of pheasants and partridges reared without the benefit of same-species parental influence. Exactly how close the parallel is between common game prey species such as these and the Chough, which is high up its own food chain, and preyed upon by only one species, the Peregrine, itself rare, is debatable but will only be answered by experience. Ryves (1948) and Ratcliffe (1980) believed that the Peregrine did not pose a significant threat to Choughs (see also Section 3.4.5a). Re-establishment in Cornwall will inevitably be a long term project, as Young & Hussain (1990) said in relation to the Cheer project in Pakistan "[b]ecause no long-term pheasant reintroduction programme has been attempted before, we have had to learn from our mistakes".

7.3.3 CAUSES OF EXTINCTION IN CORNWALL

The principal causes which I believe brought about the extinction of the Chough in Cornwall are summarised in Table 7.2.

Table 7.2 The causes behind the extinction of the Chough in Cornwall

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1 An east to west decline in southern England left virtually a relict population isolated in Cornwall. The decline in England was progressive and probably the result of harmful human influences, principally land-use change, on habitat; Atlantic oceanicity and a more primitive or independent Celtic human economy to the west helped to slow the decline.

2 Isolation in Cornwall with little or no genetic exchange with France and Wales prevented population recruitment.

3 Deleterious human land-use eventually took effect in Cornwall, resulting in retreating outposts in West Penwith and on the north coast.

4 Decline of tin-mining and coastal crofts drastically reduced beneficial coastal grazing and allowed encroachment of scrub.

5 Direct and indirect human persecution (egg-collecting, specimen- and trophy-hunting, robbing of nests for young, inadvertent trapping in rabbit-gins etc.) exacerbated the harmful agricultural changes.

6 A lack of off-shore islands, especially farmed ones, allowed no refuges or sanctuaries.

7 Finally, No. 1 prevented recolonisation after protection.

7.3.4 RE-ESTABLISHMENT STRATEGIES

If the hypothesis 'Cornwall can again support a viable population of wild Choughs' is accepted within reasonable confidence limits, what are the available options for re-establishment? They are summarised in Table 7.3.

Table 7.3 The options available for re-establishment.

1 Do nothing: wait and hope for natural recolonisation. This is obviously dependent upon at least one pair arriving together; to form a viable prospect, further genetic input would need to be forthcoming. With a sedentary species like the Chough, such an eventuality is highly improbable.

2 Option 1 + constructive land management. In other words: hope for natural recolonisation while working to provide for optimum conditions in which arriving potential recruits would settle. This option sounds attractive but it is probably fundamentally flawed, in that it would be necessary to be able to prophesy precisely the landfall point of immigrant birds. As the Rame episode showed (Appendix IV), this is not possible.

3 Physical introduction of founder stock. The various sub-options are: (a) release of (sub-)adults into a suitable site or sites; (b) controlled release of captivity-dependent adults; and (c) controlled release of sub-adults, preferably bred on site with parents (captive-bred) retained in natal aviary.

Option #3 is considered to be the only realistic option if the aim to re-establish the Chough in Cornwall is to be more than just a pipe-dream; a supposition reinforced by the unfortunate outcome of the Rame study (Meyer 1990, see Appendix IV). Sub-option #3a is (with captive bred birds) high risk, potentially wasteful, and cannot be recommended; #3b concerns birds which would be 'state-' but not 'site-imprinted' (*i.e.* conditioned to a captive state, dependent upon protection and requiring supplementary feeding, but not imprinted upon a natal site, they would therefore lack necessary survival skills and be more prone to straying); it is probably not sustainable except under exceptional circumstances. The third sub-option (#3c) has the best chance of success since it is the most controllable and would ideally involve birds with fidelity to site and parental presence.

An inevitable question posed by the adoption of Option #3 would be: from where would the founder stock be obtained? Choughs are fully protected under the Wildlife and Countryside Act 1981 and in Annex I of the EC Directive on Wild Birds (1985). Accordingly, wild-caught European Choughs are not available and translocation not possible at the present time. The option to obtain birds of alien racial origin outwith Europe would be resisted by legitimate scientific and conservation concerns. The use of alien races within a project to restock the Great eagle owl population in West Germany has been criticised Wirth (1990). The alternative is the use of indigenous captive-bred stock (7.3.5).

The source options for stock are: (i) rationalise current *ad hoc* effort; (ii) maximise potential of available captive stock; and (iii) supplement captive stock with wild 'material'. Rationalisation (source option #i) should include a full genetic and demographic study (Mace 1986), even so it would not fully exploit the existing resource unless it integrated option (ii), which requires input from keepers and breeders currently outwith the project in order to maximize the available gene pool. There is a danger associated with this option, namely: unless keepers come into the project voluntarily an illegal trade in wild Choughs could be encouraged. There is a long history of exploitation (witness the current captive population) and this is not yet wholly ended. The market creation danger has also been recognised in relation to exotic pheasants (Garson 1990). The goodwill of registered keepers must be sought and they should be encouraged to join the project.

Option (iii) would not conform to NCC and IUCN guidelines unless it could be shown that collection from wild sources would be likely to have no destructive effect on remaining wild populations. It would then require a recommendation from NCC to the Department of the Environment to grant a licence. Overall, it would need to be confirmed that an attempt to re-establish the Chough in south-west England was a feasible and desirable objective for the conservation of the species. Scientifically, there is no reason why Option (iii) should not be considered. A possible scenario might involve a minimal yield of 1 egg per nest from sites which consistently fail; such eggs could be incubated artificially or cross-fostered (Fyfe *et al.* 1978, Dixon 1986) possibly by Jackdaws or doves. [Embryonic imprinting is not known to occur with altricial species (O'Connor 1985).]

If a 'doomed surplus', caused where natural mortality is determined by population density, seasonal food availability or some other naturally occurring limiting factor (Perrins & Birkhead 1983) could be identified (*e.g.* regularly failing nests), a scientific, biological and conservation resource could be created, which would have as an additional side-benefit the lessening of natural wastage at the site of wild origin. The offspring so produced could be used either as captive founder stock or as release material. However the situation would be paradoxical in that such a doomed surplus might consist of individuals of lower genetic quality; if so while this would reduce the consequence (were they to survive) to the original gene pool, it would also engender low quality input into a wild founder population, perhaps the very thing one would wish to avoid. In any event, such a measure could only be justified if it could be reasonably shown to represent no serious risk to stable wild populations. On the other hand, It would also be useful to know whether Choughs, normally single-brooded, can compensate for occasional egg loss, and whether they can 'double clutch' if they lose a clutch soon after production, as is suggested by Ralfe (1905).

As a footnote, it is perhaps worth pointing out that bird-protection originated to protect birds against deliberate exploitation and not against constructive initiatives. This was well expressed by Frankel & Soule (1981) "Designed to protect or limit the commercial exploitation of wildlife, [these] statutes also effectively cripple legitimate scientific activities that can increase our knowledge and help to protect rare and endangered species".

7.3.5 CAPTIVE BREEDING

Captive Choughs are available to conservation because Choughs have been maintained in British zoological collections since earliest times due in large part to their popularity as pets (Chapter 3). The present captive population of Choughs is a valuable resource. With development of the breeding programme, it will increase and help to reduce the threat to wild populations. However, there must be safeguards and, accordingly, Frankel and Soule (1981) recommended *Designated Captive Breeding Programmes*, which, in summary, advises that (i) target species should be truly endangered and that extinction would have cultural or ecological impact; (ii) the programme would enhance survival prospects; (iii) data would be recorded to the highest standard and made available to all *bona fide* parties; (iv) a *breeding plan* would be agreed to meet certain genetic, demographic, behavioural, veterinary and husbandry standards with expert consultation; (v) there would be binding agreement between cooperating institutions to the *breeding plan*; and (vi) there are means to monitor progress and accountability.

This section is intended as an overview to captive breeding programmes and discusses their general relevance to *Operation Chough*. All captive breeding programmes involving rare fauna should have an international studbook base (G. Mace pers. comm.). The very first studbook for an endangered species (European bison) was established in 1932, but it was another 30-40 years before the ethic became established. Seal (1986) succinctly discusses captive propagation goals and considers that by the year 2000, there will be a need for about 500 studbook-like programmes (in 1984 there were 61 (Glatson 1986)). The relatively recent growth of interest in captive breeding programmes, as tools for conserving species threatened by habitat deficiencies, was reviewed in 1975 by Martin; Cade (1986) examined exhaustively all projects (mainly in the USA and Europe) concerning diurnal raptors. [Professor Cade is well-known for his work on Peregrine and Bald eagle rehabilitation in ~~the~~ North America.]

Georgina Mace (1986) outlined the genetic problems besetting small populations in captivity (see also Soule 1980). She concluded that although small founder populations might be comparatively as genetically diverse as larger populations, which have reduced sets of alleles due to genetic drift caused by successive captive generations, the general maxim that the greater the number of individuals, from a range of sub-populations and genetic backgrounds, the better will be the chances of maintaining a maximum of the pre-existing genetic diversity. Foose (1983) described the aim of 'zoo-banks' as "maintenance of the maximum amount of genetic diversity available in the founder stock that has evolved in wild populations". Matthews (1973) expressed some of the difficulties in relation to waterfowl, a family with which there has been some success.

The problems are not only genetic. With regard to behaviour, Monaghan (1990) points out that like many corvids, Choughs are highly social birds, and that keeping social animals in captivity can give rise to many problems. It is easy to see that young and inexperienced birds, even if released directly from a natal aviary into a suitable habitat are going to lack important survival skills such as predator avoidance: an increasing problem with the expansion of the Peregrine, in Cornwall as in North America. Monaghan also mentions the possibile adverse effects on sexual and social behaviour in individuals deprived of natural filial and sexual imprinting. It obviously behoves keepers of such species in captivity to consider very carefully the structure of their groups (*ibid.*). However, most research into social structuring of Choughs has been carried out on Islay, where large communal roosts occur and the Chough exists at a comparatively high density (Still *et al.* 1986), which is not the case in West Wales. It is a matter of conjecture whether the two situations are fundamentally analogous, and whether empirical data derived from one should be applied to the other. Where there is an absence of complex social gatherings, it is difficult to see how truly comparable data can be gained. The social structuring of Choughs in Wales remains largely unknown.

At present, 25 captive individuals are available to *Operation Chough* from which it is hoped to breed a nucleus founder stock for re-establishment. These are a miscellany of genotypes although, so far as is known, all of the nominate north-western race. They were acquired over a period of many years from legitimate sources, and are mainly of avicultural origin pre-dating legislation. Although, as mentioned above (7.1), captive breeding programmes have been employed with considerable success with waterfowl and pheasants, and with owls too (von Frankenburg 1974, Warburton 1984, von Frankenberg und Ludwigsdorf *et al.* 1984), breeding results within *Operation Chough* have so far been poor, and only one person within the UK has apparently mastered the technique of successfully breeding Choughs in captivity. One of the main problems in the past has been differentiating the sexually monomorphic cohorts, but this has now been successfully resolved by the use of laparoscopy (see also Figure 1.5). Remaining problems concern areas such as incompatibility between sexes; incorrect sex ratios in sub-adult and non-breeding groups; timing and methods of pairing birds; housing architecture (size, degree of seclusion and isolation from cohorts and external stimuli etc.); nest location (degree of exposure/darkness etc.); diet - quantity, mode and regularity of serving (*ad lib* causes less disturbance but discourages hunting stimului and exercise etc.).

No difficulty in maintaining bodily condition has been experienced: Choughs will take a wide variety of easily obtainable foods, however, when kept in seclusion and deprived of external stimuli, obesity and diminished fitness can result (pers. obs.). Incorrect age and sex ratios should, with the acquisition of more stock and the passage of time, have been corrected (Woolcock 1990). When all else fails, semen collection and artificial insemination (Boyd 1978, Brock *et al.* 1984) have been used successfully with species far smaller than the Chough: *i.e.* parrots and finches (Samour 1986), but it is time-consuming and stressful to the bird (Luthin *et al.* 1986).

If and when young, intended for release into the wild, have been produced in the past, their imprinting on humans has often been a problem. But work on non-passerine species is beginning to pay off: for example, that carried out on visual and auditory isolation-rearing at the International Crane Foundation (*op. cit.* for a comprehensive review). Increasingly, fledglings are fed from behind blinds with glove puppets. Jones (1981) discussed socialisation problems with raptors, and indeed much of the experience has been with raptors. Rearing young in creches shows promise

(C. Jones pers. comm., Bruning 1984, Martin 1984), and Jones (1984) believes that falcon chicks must not be allowed to become over-hungry.

Undoubtedly, there will be survival deficiencies when aviary bred birds endeavour to take their place in the wild, and undoubtedly there will be losses. Whether or not these are sustainable cannot be answered until a pilot project is underway. The captive bred Chough currently living on the North Cornish coast appears to have survived for several months satisfactorily but others, it is believed, have perished. It is undoubtedly tricky playing at God: deciding which species to help and which to abandon, but Seal (1986) reminds us that "Not to act is to act. The necessity for action always presents the possibility of unpleasant alternatives".

7.3.6 POTENTIAL RE-ESTABLISHMENT SITES

The three Cornish study areas, described in Chapter 2, were selected within regions believed most able to sustain re-establishment. To recap: these were regions known to have previously supported good Chough populations, and which retained elements of habitat quality similar to those used by Choughs in West Wales. The areas were: C1/North Cornwall (Tintagel - Park Head), C2/West Penwith, and C3/The Lizard (Figure 2.1). I have endeavoured in Table 7.4. to set out qualitatively the principal merits and demerits of each site in much the same way as Anderegg *et al.* (1984) convincingly did for potential release sites for the Lammergeier in the Alps.

The Lizard peninsula emerged as the leading contender despite scoring

Table 7.4 Merits and demerits of potential Cornish re-establishment sites. Merits emboldened

Site	Comments
C1/ North Cornwall	**Includes area of latest occupation. Long stretch of coastline, with necessary variety of elements, extending in the south to C2 and in the north to Devon and beyond. Closest region to existing range (and the possible Lundy Island staging post), and therefore the most the likely first landfall of natural immigrants from Wales. Accommodates some very sympathetic farmers and land-owners, and stretches of wild relatively unpeopled coast, which increase northwards beyond Bude.** No obvious focal point for concentration of effort. Possibly no discrete landmass of sufficient size to support more than scattered pairs during early stages. Security risk: difficult to wardening and monitor progress of birds. Likely disturbance: supports popular tourist towns, *e.g.* Newquay, Padstow and Tintagel; climbing locations and other outward-bound traffic; and continuous coastal footpath.
C2/ West Penwith	**Abuts C1. Large discrete ESA (Environmentally Sensitive Area) with 'good' blend of appropriate low-intensity mixed agriculture: many small fields (*ipso facto* many walls); traditionally supports outwintered cattle. Possibility of aid for participating farmers under various schemes, *e.g.* 'set-aside'. Highest and most varied proportion of coastline to landmass, with continuous south- and north-facing coasts including good NT owned reserves. Centre of historic Chough range in Cornwall; between other 2 contenders. Mild climate, high exposure. Large numbers of tourists are a source of funding and can, with care, help to create Chough-friendly conditions.** Mixed ownership: possibility of diluted management. The most popular tourist region within Cornwall, and suffers most concerted and exacerbated pressure of all over entire area. Lands End is centrally situated and attracts over 1m people p.a.; such high levels of tourism usually create problems of erosion, habitat degradation and disturbance. Extremely low or absent sheep population.
C3/ The Lizard	**Large discrete area with mild climate, a variety of exposure aspects from due east to due west over long and rugged coastline. Largely under management, *e.g.* NCC, NT, MOD and private owners sympathetic to the overall aims of re-establishment and offering indefinite continuity. Long tradition of rough-grazing on cliffs, continued now partly for conservation reasons including Choughs. Low tourist pressure generally. Extremely important scientifically; the best heathland site in Cornwall, subject of several specialist studies, *e.g.* Malloch (1971), Hopkins (1983) and Hughes (1990); unique geology which provides a great range of crevices, unlike C1 and C3. Forms part of continuum between Rame peninsula in east Cornwall (site of recent natural occurrence), Looe Island and C2, about 40km distant. Nearest landfall site to Brittany. Good security prospects and opportunities of aviary seclusion; the region is already ably wardened. Accessible to the *Rare and Endangered Birds Breeding Centre* at Hayle, which houses the nucleus founder stock.** Emerged poorest of the 3 Cornish sites in terms of invertebrate species-diversity (but see Chapter 5.3.4). Choughs disappeared earlier than from C1 and C2 (see 3.3.1). Site most dissimilar to and farthest from regions of occurrence in Wales. Botanical rarities would restrict grazing in some areas.

least well in invertebrate diversity at sites identified as prime potential feeding areas (Table 5.8). However, all Cornish sites surpassed the Welsh ones in this respect, and when background invertebrate abundancies were analysed (*i.e.* in areas adjacent to the former but considered marginally less favourable), the Lizard scored higher than anywhere else (Table 5.10; and see Chapter 5.3.4). It is furthermore possible to conclude that a flock of Choughs established on this peninsula would be able to expand westwards via West Penwith (a distance of *ca*.40km across Mounts Bay) to North Cornwall or directly overland (*ca*.50km). Bullock (1985) inspected blocks of land within the same areas, and also considered the Lizard to be the foremost site.

7.4 HABITAT MANAGEMENT

Changes in land-use and extensive removal of domestic herbivores from the cliffscape, coupled to the decline of the Rabbit population following myxomatosis (Sumption & Flowerdew 1985), has led to vegetation changes on a huge scale in Britain (Mitchley 1990). Mitchley gives an example of the knock-on effects: wild White clover seeds were added to commercial grass seed mixes at the beginning of this century with the consequent improvement of inbye land (near the farmstead) and abandonment of outbye land including the semi-natural maritime clifftop vegetation with consequent deterioration.

The vegetation changes pose severe problems for conservation management; and the problems are particularly pronounced in the seacliff landscapes of southern Britain, where the decline in domestic grazing and the consequent overgrowth of cliff-tops with coarse grasses, bracken and scrub has been widespread. Mitchley ponts out that the conservation manager has to devise management solutions to these problems.

In the main, the following recommendations apply both to the conservation of existing Chough populations and re-establishment in Cornwall:

1. Continue and extend Welsh population studies, introducing as a matter of urgency, a coordinated colour-ringing programme, extended from the Islay and Bardsey programmes, in order to monitor survival and dispersal. Even if the feasibility of re-establishment is not accepted at the present time, data from such studies would be useful for future proposals and for the conservation of wild populations.
2. Where lapsed, restore coastal management, as set out in Table 7.5, in order to deter blanket scrubbing and encourage a mosaic of

different habitat types (hitherto identified as important by Donovan 1972, Gamble 1984, and Bullock *et al.* 1986; see also Chapters 4 and 5). Increase stocking levels of sheep (and/or goats) to levels comparable to areas of Wales which support higher levels of Choughs, *e.g.* the Lleyn peninsula (G. Roberts pers. comm.).

3. Create earth exposures by whatever method is appropriate; this may be within usual regimes of land management, or by more eccentric, site-dependent methods, if not damaging to other biological systems.

4. Limit disturbance. Although human pressure can have beneficial side effects in creating low profile vegetation and exposure zones (*e.g.* along paths through rank growth), disturbance at breeding sites from April to June is a serious problem (6.4). Plans to reroute or create new coastal footpaths should avoid traditional nest-sites during the breeding season. Dogs *must* be controlled near key feeding areas and traditional nest sites; this is also necessary to prevent the worrying of stock and promote farmer co-operation

5. Create 'island' refuges. Promontories, headlands and capes can be managed virtually as islands and protected from undue human disturbance. The ESA initiative extends this possibility.

6. Supplemental feeding has been shown to be valuable in the conservation of endangered species such as the Mauritius kestrel (C. Jones pers. comm.). Such a strategy with newly-released Choughs could help pioneers through difficult acclimatizatory periods, *e.g.* during severe weather and droughts. Supplemental feeding for a predominantly insectivorous species could involve provision of mealworm *Tenebrio molitor* larvae at traditional points such as at the natal aviary; see also Recommendation #9 in Table 7.4.

Table 7.5 Land management objectives for application in Chough and prospective Chough areas.

	Objective
1	Open maritime cliff/*Armeria*/therophyte communities maintained by geological structure, exposure to prevailing winds and/or grazing. A combination of such pressures will create rich and varied mosaics of vegetation (long and short), dung enrichment, trampled paths, and earth exposures
2	Semi-natural well-grazed maritime and species-rich grass communities, such as '*Festuca-Plantago* swards'
3	Low intensity mixed farming regimes
4	Grazed wall-banks
5	Managed but unploughed pasture (rough, unimproved or semi-improved)
6	Scarification of ground where possible in place of ploughing
7	Localised and strictly controlled 'cool' burning or swaling
8	Out-wintering of cattle, where not deleterious to botanical or other considerations
9	Strip-cultivation of non-harvested cereals as conservation measure to provide supplemental food in late summer and autumn (also carrying additional benefits to other wildlife); such areas could be rough grazed
10	Avoid burning stubble; encourage 'untidy' or 'eccentric' farming in critical areas, *e.g.* leave spillages *in situ*, and field headlands unploughed.
11	Avoid usage of biocides, including antiparasitic 'Ivermectin-types'

7.5 DISCUSSION

The results of this project suggest that the extinction of the Chough in Cornwall was caused by human persecution (seemingly at a far higher level than elsewhere within its British and Irish ranges) exacerbating unsatisfactory habitat changes caused by agricultural improvement and general coastal degradation following the decline of the coastal crofters and miner-farmers. The absence of island refuges, and the remoteness of contiguous populations in Wales prevented natural recolonisation.

The dye had been cast before the tithe surveys in the mid-C19, and were it possible to know the status of the species in West Wales prior to this, a similar picture might be found there. By the 1840s, though much reduced in Wales, the Chough was hanging on, no doubt bolstered by dispersal from the north and local islands. Here the species continued to survive at a low level, in much the same way as happened in Brittany, where there were also island sanctuaries.

Before addressing the key question 'Can Cornwall again support a viable Chough population?' we should be sure that it is a good idea. A question originally addressed in Table 1.2. It would be wrong to describe the Chough as an endangered species even though it is extinct in England, and globally there are certainly many more deserving cases in need of conservation. However, the efforts to protect it are a genuine and sincere response from local people who associate with the species, and are prepared to finance efforts to help it; they might be less likely to put that money into less immediate projects. Since the funding is locally generated it is not conflicting with other nature conservation priorities. Leaving aside, for the moment, local, cultural and sentimental reasons, it may simply be restated that the Chough is (i) a valuable indicator of a healthy cliff environment; (ii) a benign species without any of the vermin connotations that are commonly associated with other crows; (iii) protected throughout Europe, specially so within Britain; and (iv) within NCC criteria for acceptable re-establishment as an act of constructive conservation. Furthermore, its revival in Cornwall (=England) would reinforce its status in Britain and NW Europe generally.

As to feasibility, the short, safe answer is 'maybe' but can we be braver and more accurate than that while retaining objectivity? The easiest and least contentious recommendation is wait-and-see/hope-for-the-best, and this would certainly please the purist who would rather see a species die out than be interfered with; against this is a not unreasonable theoretical argument that man has been interfering with species ever since he first learnt to use fire and the stone axe. The NCC explicitly acknowledged this in its Corporate Plan 1986-1991 (Theme 8: Constructive conservation (NCC 1985)). The occasional appearance of vagrant Choughs in Cornwall (Darke 1971) supports both the 'do nothing' and 'helping hand' factions but it is improbable to expect enough vagrants to converge on the *same* bit of *suitable* coastline at the *same* time. The two birds which appeared at Rame in 1986 (Meyer 1990, see Appendix IV) might well have founded a successful outpost had there been other pairs stationed along the coast as is the case in Dyfed. After the death of one (believed to be female), the remaining bird spent 3 weeks patrolling the coast before apparently drifting away westward along the coast and thence possibly up the Fowey estuary, for it was last reliably reported (and the evidence of its feeding witnessed by me) in a steep pony-grazed field near Bodmin in central Cornwall (T.O. Darke pers. comm.). If the bird maintained this orientation, it is tempting to speculate that it might have gone to West Wales, perhaps from whence it came.

One captive bird of an unknown number released covertly without *Operation Chough* knowledge in autumn 1990, remained faithful to a stretch of coast near Port Isaac in North Cornwall at least until the time of writing (March 1991); one other is known to have died (S. Christophers, M. Ellis, A. Langdon pers. comm's.). It is a feature of Chough vagrancy to Cornwall that birds are seen on different stretches of coast, *e.g.* the north, West Penwith, Mevagissey, Looe and as far east as Plymouth. Viewed in this light, natural immigration represents an unfortunate wastage of genetic stock. Even one population centre would provide a focus for wandering birds and a reservoir of genetic material to support others.

How feasible is the founding of a population focal point? Of all the available sites with a good historic record of Chough activity, the Lizard peninsula was considered by Ian Bullock in 1985 as the "most promising", with this I concur. Whether localities other than the Predannack region sampled during the present study are contenders is a matter for discussion between interested parties and local land-managers. I would, on the basis of two visits, recommend further consideration of the cliffs around Kynance. Ian Bullock (*ibid.*) rated this section of coast the most highly of all those NT properties he visited, it is though subject to higher visitor pressure than the Predannack site a little to the north; Bullock did not consider the heavy pressure at Kynance a problem, indeed he also pointed out the beneficial side-effects of human trampling noted during the present study. The consensus of available opinion is that the western Lizard coast offers the best hope for successful recolonisation. It is a National Nature Reserve and has largely multiple sympathetic ownership; there are bioclimatic and geological advantages; a variety of aspects; and it occupies a centrally strategic yet remote position within Cornwall.

The work needed to create favourable habitat for Choughs on the Lizard, if sufficient does not already exist, would involve extension and development of current management policy: a continuation of the burning and pastoralism, extending this and increasing stocking rates where necessary consistent with constraints imposed by conflicting nature conservation interests (in this case botanical) in order to improve the invertebrate prey-base and its accessibility to Choughs. Managed sensitively and pragmatically, any advantages accruing to Choughs would also benefit the lower trophic levels of the area and increase species diversity.

The long-term feasibility of re-establishment involves more than a trust in the suitability of habitat quality. There will be a need to monitor released birds by counts and perhaps telemetry, and certainly a need for careful wardening and observation of survivorship, especially in relation to possible Peregrine predation. There will probably also be a need to provide back-up care in the form of supplemental food (or at least retain this option and monitor the conditions which would trigger its implementation), guard those feeding-, roosting- and nesting-sites shown by monitoring to be of crucial importance during the early years of actual re-establishment.

The presence of recolonising Choughs on the Lizard would inevitably lead to increased public interest in the area, and this would incur both the costs and benefits common to many other sites of great natural and public interest. Financial benefits could be utilised to safeguard the area for the benefit of all wildlife, and there would exist an opportunity to manage the pressure in a constructive way rather than as damage limitation. Sufficient funds should initially be forthcoming from local and business interests to prevent the project from creating problems of conflicting priorities. A fixed observation centre with video monitoring equipment would serve both scientific monitoring and public interest; it would help to prevent excessive disturbance and provide educational opportunities. Such facilities could be linked to off-limits captive stock so as to minimise their disturbance, provide security and a point of continual interest for visitors.

8 GENERAL DISCUSSION

It was stressed at the outset that a vital part of conservation is a knowledge of the factors that limit the distribution of rare and endangered species. Many species-orientated 'rescue' projects have to confront the fact that the ecological requirements of their subjects are somewhat less than fully understood; there is also a requirement to understand the reasons behind declines. Usually the two are related. Research objectives such as these are fairly self-evident and usually at least tacitly acknowledged, but they are beset with difficulties: not least of which is the fact that the species concerned may have either already disappeared or exist at such a low ebb that their behaviours and apparent requirements may not be typical.

The habitat of a terrestrial bird population is usually defined by the ecologist and not by the ornithologist (Perrins & Birkhead 1983). This is because the fauna directly or indirectly depends on the first trophic level for its energy source, and this is always vegetation, usually a green plant or other autotroph which traps photo energy and converts it to available energy. This first level is controlled by various edaphic factors, only subsequently being used and shaped by consumers, *i.e.* the occupants of higher trophic levels.

Sometimes, the habitat or area supporting the individuals of a population is well-defined and obvious due to physical characteristics: classically, a small remote island or atoll. Where a population occupies a less obvious territory, an understanding of the ecology of the area needs to precede its definition and autecological study of a constituent species.

A tit, for instance, may occupy a 'realized niche' at a particular height within the canopy of broad-leaved woodland but without an understanding of stratification within the woodland, knowledge of the tits occupying it will never be complete.

The Red-billed chough inhabits both islands such as Islay and Bardsey and also the continental Eurasian landmass. Several geographical races have been described. It is perhaps interesting to note that more sub-speciation exists in avifauna, which are (like taxonomists) principally visual creatures, than in mammals. Were Choughs mammals, there might be fewer so-called races and fewer problems when speaking of translocation; on the other hand, the Choughs of Islay may, in their 'realized' ecology, be substantially different from the Choughs of West Wales, or they may represent 'micro-geographic races' (Mayr 1959).

Whatever the outcome of such taxonomic arguments, the Chough *is* locally rare and specialized: a sedentary species limited in its distribution not so much by physical boundaries but by special habitat requirements. Clearly, in order to better protect those living in mainland Wales, it was necessary to undertake specific research there; and also to assess the feasibility of re-establishment in Cornwall, since Wales is the closest region, in terms of both distance and physical characteristics.

Unlike previous autecological studies of the species, which have all taken place within island strongholds, the population under study here was thinly and linearly distributed along a mainland coastline, which provided many obstacles to sustained continual monitoring. The population was at a very low level: *i.e.* 7 pairs in >100km of coast, separated into 4 blocks for the purposes of this study. Viability is assumed because of traditional occupancy but flock sizes seldom exceeded those of family units, *i.e.* 5-6 birds (except at Marloes, where 8-9 was common), and birds were often present only in pairs.

The paradox of the Chough in Britain is that it both needs man and yet shuns him. In this sense it is a throwback to old pastoral agriculture, when humans and their livestock occurred throughout the wilder regions and when scarcely an inch of countryside was unused. Modern farming derives extraordinarily high yield from minimal acreages, and results in a countryside either so heavily exploited it sustains little if any wildlife, or so neglected that it reverts to scrub. Neither of these options provides a species like the Chough with a viable resource, but in areas where a more primitive agriculture still survives, the Chough may find a precarious existence.

Pastoralism is essentially the use of grazed land in support of livestock and a means of farming. Without meat to eat, milk to drink, or leather and wool for clothing, livestock would hardly be needed and there would be no pasture. The patchwork of enclosed fields, so traditionally a part of Britain and so beloved by many people, would be replaced by prairies of wheat, as has already happened in East Anglia; the sheep-grazed fells, downs and hills would be blanketed in scrub. Not only would the landscape alter radically, wildlife diversity would be much poorer. The decline of the Chough would be rehearsed with all other fauna and flora which evolved with and now depends on grazed grassland (*i.e.* pasture).

The Chough, used in heraldry and symbolically from the earliest times, and now recognised as a flagship species by official conservation bodies concerned with the maritime cliffscape, has perhaps still another role to play, as an harbinger for the greater countryside, a symbol for the need to return to a saner method of farming: 'less input - less output - more diversification'. It may be re-stressed here that the Chough was once an inland species and occurred across much greater tracts of countryside than is now the case.

While there is no doubt that coastal low-intensity pastoral systems (see, *e.g.* Bignal & Curtis 1989) form an indispensable component within the Chough's present-day overall habitat requirements (the 'functional unit'), it is thought that the species evolved in montane regions and spread to coastal districts in western Europe (Guillou 1981). The results of my behavioural studies, while requiring further work, indicate that the species, in western Europe at least, performs marginally better in natural cliffscape than in pastoral agriculture. The species selects the former preferentially, and foraging success and efficiency are superior, even than in pastoral agriculture managed to suit Choughs. Componental examination of the habitats associated with Chough feeding events showed that those most consistently selected were more likely to be the product of natural abiotic forces rather than of pastoral agriculture: bare earth (identified in >40% of all feeding occurrences), maritime therophyte communities (nearly 16%) [bare earth is a consistent factor within therophyte communities], rock-vegetation/earth interfaces (28%), cliff crevices (>21%). The top five preferentially selected broader habitat categories were all primarily the product of natural forces, not man: cliff-slopes, maritime grassland (except where grazed by domestic animals), ant-created habitat, species-rich grassland and therophyte zones. Sheep-grazed grassland, the most frequently selected man-created habitat, was used in 15.4% of all feeding events.

After retreat to the cliffs, any reduction in available substrate would have made Choughs increasingly dependent on man and his agricultural practices nearby. While these were in a semi-natural state, Choughs could have compensated, but with increasing intensification, the ploughing up of heathland, the introduction of monotonous rye-grass/clover swards, the profligate use of artificial fertilisers and herbicides, the in-stalling of cattle, and the growth in cereal farming, their survival became increasingly difficult. Moreover, where this was compounded by direct persecution, such as hunting with increasingly sophisticated weaponry (muzzle loaders were replaced with breech loaders etc.), the collecting of eggs and specimens (live and dead), incidental disturbance caused by the advent of tourism during the Victorian age, the motor car and railway train, plus other hazards, *e.g.* gintraps for rabbits, survival became at times impossible, and the species rapidly retreated across southern England and became greatly reduced even within its western seacliff stronghold (see, *e.g.* Rolfe 1966, Darke 1971, Donovan 1972, Penhallurick 1978, Balchin 1983, Bullock *et al.* 1983a, and Owen 1985).

So is the Chough a species of the seacliffs or of pastoral agriculture? The simple answer is 'both', but that is only a description and not an explanation. Broad-based habitat assessment, as undertaken during this study, should be replaced by improved techniques of cliff assessment on a scale which relates to Chough behaviour, *i.e.* their ability to exploit complex mosaics, and small patches/zones of optimum habitat. I wish here to draw together elements from the preceding chapters and explain, by virtue of their separate aims, the different facets of the Chough's habitat requirements in West Wales, and then to relate these to a hypothetical situation in Cornwall. Realisation of the fact that Chough usage of pastoral components is greatly influenced by cliff quality reduced the need for precise descriptions of contiguous farmland. Therefore, to manage Chough populations it is probably better to aim for a high quality cliffscape rather than rely on neighbouring agricultural management outwith conservation areas.

The kind of conservation measures needed are much better understood now than they were even in the eighties. Jonathan Mitchley (1990) has produced a timely and cogent Sea cliff management handbook for Great Britain which illustrates the complex nature, ramifications and side-effects of management. Under the heading "Restoration grazing management" Mitchley gives the following options "(i) [re-]introduction of grazing after variable periods without grazing, (ii) increase in stocking rate, (iii) decrease in stocking rate, and (iv) removal of grazing altogether". He cites the Chough and Large blue butterfly *Maculinea arion* as examples where the restoration of grazing is designed to improve the habitat. The decline and ultimate extinction of the Large blue has a parallel with that of the Chough in both local geography and timescale (Thomas 1977). A common reliance upon ants of the *Myrmica* genus, and the susceptibility of these to the sort of habitat changes that are known to affect Choughs directly, serve to illustrate the fundamental effects of habitat change on the higher trophic levels. However, the introduction of grazing onto natural communities or those in which the influence of man is secondary to natural maritime exposure can seldom be justified. Elsewhere, the history of sites, and the full implications of restorative grazing management must be planned very carefully and frequently monitored with the support of fixed point photography.

In this study, a detailed botanical investigation of key feeding sites revealed a predominance of edge zones and ecotones; the *Aira praecox* sub-community of the *Armeria-Cerastium* maritime therophyte community being, by far, the most frequent type. *Aira praecox* (Early hair-grass) was found growing in 56.8% of the 58 quadrats surveyed, but represented a mean cover of only 1.4%, tending to confirm it as an indicator species. The main cover-types within this survey were *Festuca rubra* (Red fescue) (15.5%) and exposed substrate (14.1%); no other cover-type exceeded 5%. Evidence of sheep grazing (*i.e.* dung) was found in 17.2% of the samples surveyed but dung represented only 0.3% cover, a factor exceeded by rabbit dung (=0.5%).

Rabbits were a far greater grazing pressure before the outbreak of myxomatosis, their dramatic reduction in the 1950s exacerbated an already deteriorating situation (Sumption & Flowerdew 1985) which had begun with the abandonment of many crofts and the decline of domestic herbivores such as draught horses and pit ponies on cliff headlands during the C19, a process complete after World War II (see, *e.g.* Roberson & Stamp 1941, Balchin 1983, Mitchley 1990). Where present in reasonable numbers, as at Newgale-Solva, the importance of rabbits should not be underestimated (Mitchley 1990). According to Carrington (1951, *op cit.*), 9 rabbits = 1 sheep in grazing ability. Sheep stock-rates are critical (Liddle 1975): 1/0.405ha permits tall grasses, but 3/0.405 creates a low sward. Where the fencing of cliffs is not possible due to practical, planning or financial constraints, unenclosed grazing is deterred by the risk of unleashed dogs causing stock to panic with fatal consequences. In such circumstances, rabbits or goats are an alternative which might well be considered or encouraged as part of a coordinated management approach.

Livestock create open, low profile vegetation and dung, which combine to increase the invertebrate biomass and render it available to Choughs and other wildlife. In the absence of domestic livestock, Choughs rely on abiotic factors (*e.g.* exposure) to create open conditions, and an unenhanced invertebrate spectrum. If they are to have access to soil invertebrates, there is also an apparent need for suitable conditions which do not involve prolonged and regular freeze-ups. In Britain and Ireland, where mountains and valleys do not exist as in the Chough's main Eurasian range, the species is now concentrated on and around the cliffs of western seaboards. Central to the understanding of the species is a knowledge of the factors which determine this distribution and, within it, the relevant importance of cliffs *per se* and the adjoining pastures.

Increased understanding of the role of Cornwall and Brittany in the decline of the Chough and their potential for revival will throw light on the Welsh position and help safeguard it. If the Chough were limited by bioclimatic factors alone, and the non-freeze factor was shown to be the key factor, a south to north decline in Britain would not be expected, whilst an east to west one, ending up in Cornwall, would. It seems that bioclimatic factors were superseded by human agency and revolutions in agriculture, industry, affluence, mobility and leisure. Recent stabilisation and recovery of the Chough, particularly in two areas, due to a reversal of former deleterious agricultural practices, *i.e.* Calf of Man (Bullock & del-Nevo 1983) and Bardsey Island (Roberts 1985) further support the contention that the recent decline of the Chough is associated with human agency but so is its recovery. Recolonisation of Anglesey (1958), Montgomery (1959) and Denbighshire (1962) (Owen 1989) point to a response to increasing protection.

The key factors appear to be changes in transition between landscape governed by natural and semi-natural forces. Domesticated grazing animals are a comparatively recent event in evolutionary terms. *Ad hoc* subsistence farming and low-input extensive systems would certainly have been environmentally friendly and complemented natural forces. Choughs, apparently occupying a niche with little competition, might have been expected to take advantage of human activities which extended that niche, and this is indeed what probably happened during the Middle Ages until the rate of change became too fast and too severe: a process which perhaps began in the late-C17 and accelerated until conservation imperatives began to take effect in the mid-C20. Signs that populations elsewhere in Europe (Bignal & Curtis 1989) and the Republic of Ireland (R. Nairn pers. comm.) are also under pressure indicate that extinction in England will be followed elsewhere unless comprehensive conservation measures are implemented.

As stated, the knowledge gained from this study was to be applied in Wales and related to Cornwall. Conservation of the species in Wales had not waited upon the commencement of this work. It had been a matter of concern to local conservation interests for some time. At Cemaes Head, positive management for Choughs had been in train for many years. At Strumble, the area was first protected in 1954, extended in 1977 to include Strumble Head itself, and further extended in 1988 (S.B. Evans pers comm.). These two nearby examples show that a variety of conservation measures, dependent upon local criteria, are probably both inevitable and necessary. With the Mwnt-Cemaes/Strumble duality serving as an example, it is possible to postulate an integrated system of land-use which blends traditional farming with broader conservation interests. A *mixed* grazing regime can be envisaged: employing cattle, sheep and possibly horses, for their differential grazing strategies, at variable stocking rates, and yet flexible enough to be sensitive to extrinsic seasonal demands and local constraints. Sometimes, perhaps where there is a history of grazing such as at Cemaes Head, stocking rates could be very high. The effects of less controllable resources, such as rabbits would, if present in appreciable numbers, be a bonus. Since Choughs are known to utilise burnt areas for food (Haycock & Bullock 1982), 'cool' localised burning or 'swaling' of gorse could be utilised to supplement grazing; this has historically been a common and effective way of controlling scrub and it provides 'first bite' spring fodder for livestock. And when harvested, 'furze' provides a useful domestic fuel.

In the two southern study areas (Newgale-Solva and Marloes), reduced pastoralism was possibly more than offset by increased rabbit and ant populations and increased exposure caused by slopes facing south, west or east, rather than north or north-west. The result was more bare ground receiving more early morning sunshine at an angle of dip, *ca.*45°, which achieved maximum insolation. These factors combined to the benefit of the invertebrate biomass, and, therefore, to Choughs. It was very noticeable that the only such slope at Cemaes (east-facing and therefore receiving early morning sun), albeit of a quite limited extent, was intensively used by Choughs at all times of the year.

Inevitably, the species has in the past been painted as black as other crows, but there is evidence to suggest that it is actually of benefit to man. Garcia Dory (1983) demonstrates a role, the fertilization of mountain pastures in N Spain, which might have parallels elsewhere. The high nitrogen content in animal dung kills the herbage beneath and dead circles of vegetation are numerous and widespread. Good management of such pasture would be to spread the dung and avoid excessive concentration. The Chough, Dory states, undertakes this task:

> "When the dung dries, the coleoptera establish themselves in it and their arrival attracts the birds. *Pyrrhocorax pyrrhocorax* arrives first, with its long beak it perforates the top layer of the dung searching for the beetles which are at the bottom. They are able to

> catch the biggest insects (*Geotrupes*) with their curved bill (which differentiates them from *P. graculus*)... Once the 'top of the box' is open, *P. graculus* intervenes and looks for the smaller *Staphylinus* and *Aphodius* found inside... both species of choughs shred the dung to try and find the earthworms at the bottom. This process results in the breaking up and spreading of the dung around the pasture with the consequent benefit for the plants...
>
> "Choughs carry out this work very quickly, a flock of 10-15 birds can deal with a pat of dung in a few minutes. Once they have finished ... they fly to another place to repeat the operation...
>
> "One can conclude that the availability of food for these birds is very high, almost unlimited..."

Such revelations are fascinating and make us question our prejudices. It displays the inter-dependence between different life forms, and gives an insight into the ramifications of just one predator-prey relationship. It also shows the value of broad-based studies and of cooperation between workers in different fields. The life-cycle biology of the invertebrate prey base requires better understanding for their own conservation as well as for that of their predators. Many complete their life cycle within one calendar year, and are greatly affected by short-term or erratic management. Distribution maps, of varying degrees of completeness, are available for some groups, and information at the level available for birds and plants would be a useful source of correlative information, especially as prey ranges become known to a higher taxonomic level. Although exhaustive species-lists are less important than an understanding of the one or two main prey taxa in their respective seasons (Feare 1984), it increases understanding of ecological relationships with invertebrates if vertebrate zoologists take their level of invertebrate prey identification to a species level whenever possible (A. Stubbs pers. comm.).

Such information could help to throw light on the Chough's prey selection since there are dietary components in SW Britain which are not recorded farther north or appear to be less important. For example, ants and earthworms are taken in greater numbers than in Islay, North or central Wales; this could be due to a variety of reasons: *e.g.* a response to northerly declining ant diversity, or a dietary deficiency in southern Choughs. Despite clues to the contrary (*e.g.* Ussher & Warren 1900), earthworms had not previously been acknowledged as a regular prey species. The work of Garcia Dory, quoted above, shows that earthworms are a regular component in the diet of Choughs much farther south than Cornwall. In this study, their chaetae were present in 20% of all Welsh faeces examined (n=277) and in 75% of 99 collected in a brief Cornish winter study (in Wales, the winter value rose to 29%). This apparent relatively high usage of earthworms in West Wales and even higher in Cornwall (by 'pioneer' birds) when viewed in context with apparent avoidance in the core of the northern range must raise the possibility of a sub-optimum diet. Earthworms are transport hosts for several pathogens, and they are never taken by captive birds from choice. Gapeworm is one such pathogen, and it is known to be a problem in captive birds (Keymer 1982) and of Choughs in particular (pers. obs.). It is endemic in the wild Chough population and caused the death of one of two Cornish birds (see Appendix VII). Gapeworm is of increased risk to stressed, and inexperienced or young birds not feeding as profitably as established birds (Thompson 1983, Brown & Thompson 1986, D.B.A. Thompson pers. comm.). Stress, because it is difficult to measure, is underestimated in translocation and captive-breeding programmes, although it is now acknowledged in bird-of-prey breeding ventures (Cade 1980, Haigh 1984, L. Hurrell pers. comm.).

Local people should perhaps be made aware of latent factors such as these so that too much is not hoped for too quickly. The Chough is a much loved emblem, as important to the Cornish as the Kangaroo is to Australians, and the Kiwi to New Zealanders. It is found on the logos of businesses, the badges of official departments, and the insignia of local RAF squadrons. There is also Cornish nationalism, *Mebyon Kernow*, with its roots in the ancient Stannaries; the Chough symbolises this nationalism and links Cornwall with other Celtic countries. It is a species which well illustrates a driving force behind species conservation: not merely of interest to scientists and naturalists but of real local concern, much as the White stork is to Dutch and Danish people.

If it is agreed that re-establishment of the Chough in England is a creative and benign objective, and conforms with legal requirements, the need is for a *modus vivendi* which satisfies scientific and practical criteria. The nesting habitat in Cornwall survives as it has in generations past, the invertebrate prey biomass appears richer than in Wales, and human attitudes to wildlife have changed radically. Past differences in land use between Wales and Cornwall now largely balance; exactly how these (and concomitant human practices) separately affected Choughs a century and a half ago remains a matter of conjecture but West Wales is plainly capable of now supporting the species. It is likely, though, that increased management and more grazing will be needed to restore fully functional units in Cornwall around population centres. Given the well-known deleterious effects inherent in maintaining small populations (see, *e.g.* Denniston 1978, Franklin 1980, Mace 1986), there is a need for *Operation Chough* to proceed as swiftly as possible so that problems associated with increased homozygosity of any deleterious recessive genes present in the population do not become manifest and can be prevented by out-breeding, hopefully with the wild vagrants that still appear from time to time on the Cornish cliffs.

There is a joke in Cornwall that the Duchy is symbolised by three threatened species: the tin-miner, the fisherman and the Chough. The prospect of any of these again becoming an important feature of the county's future is remote, but the revival of the wildlife emblem would be seen as a symbol of recovery from the economic blight which followed the demise of the two principal industries.

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APPENDIX I Scientific names of vertebrate species mentioned in text

Alpine chough	*Pyrrhocorax graculus*
Arabian oryx	*Oryx leucoryx*
Bald eagle	*Haliaeetus leucocephalus*
Carrion crow	*Corvus c. corone*
Cheer pheasant	*Catreus wallichi*
Curlew	*Numenius arquata*
European bison	*Bison bonasus*
Fox	*Vulpes vulpes*
Giant anteater	*Myrmecophaga tridactyla*
Golden plover	*Pluvialis apricaria*
Great bustard	*Otis tarda*
Great eagle owl	*Bubo bubo*
Great tit	*Parus major*
Hawaiian goose (Nene)	*Branta sandvicensis*
Hooded crow	*Corvus corone cornix*
Hoopoe	*Upupa epops*
Jackdaw	*Corvus monedula*
Lapwing	*Vanellus vanellus*
Little owl	*Athene noctua*
Magpie	*Pica pica*
Mauritius kestrel	*Falco punctatus*
Nene (see Hawaiian goose)	
Osprey	*Pandion haliaetus*
Peregrine	*Falco peregrinus*
Pheasants	Phasianidae
Rabbit	*Oryctolagus cuniculus*
Raven	*Corvus corax*
Red kite	*Milvus milvus*
Redshank	*Tringa totanus*
Rook	*Corvus frugilegus*
Starling	*Sturnus vulgaris*
Stone curlew	*Burhinus oedicnemus*
Titmice	Paridae
Treecreepers	*Certhis* spp.
Waterfowl (wildfowl)	Anatidae
Wisent (see European bison)	
White-tailed sea eagle	*Haliaeetus albicilla*
Wood-hoopoes	Phoeniculidae

APPENDIX II Ordanance survey coordinates of 1km squares used in basic habitat survey

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St Brides Bay (Wales)

SM7707
SM7708
SM7709
SM7725
SM7903
SM7907
SM7911
SM7923
SM7927
SM8003
SM8011
SM8105
SM8106
SM8109
SM8125
SM8222
SM8307
SM8311
SM8323
SM8327
SM8402
SM8501
SM8509
SM8513
SM8517
SM8518
SM8521
SM8525
SM8613
SM8703
SM8707
SM8711
SM8715
SM8719
SM8723
SM8801
SM8909
SM8913
SM8917
SM8921
SM8925

Strumble-Cemaes (Wales)

SM8839
SM8936
SM8940
SM9138
SM9140
SM9336
SM9340
SM9439
SM9534
SM9736
SM9938
SN0136
SN0140
SN0338
SN0439
SN0536
SN0540
SN0541
SN0738
SN0742
SN0843
SN0940
SN0944
SN1142
SN1146
SN1344
SN1348
SN1546
SN1645
SN1649
SN1650

Cardigan-Newquay (Wales)

SN1847
SN1851
SN1952
SN2049
SN2247
SN2251
SN2351
SN2449
SN2647
SN2651
SN2849
SN2953
SN3051
SN3253
SN3255
SN3451
SN3455
SN3653
SN3657
SN3658
SN3855
SN3859

West Penwith (Cornwall)

SW3425
SW3523
SW3526
SW3528
SW3532
SW3623
SW3627
SW3631
SW3721
SW3734
SW3821
SW3825
SW3829
SW3833
SW3936
SW4022
SW4023
SW4027
SW4031
SW4035
SW4225
SW4229
SW4233
SW4237
SW4423
SW4427
SW4431
SW4435
SW4439
SW4625
SW4629
SW4633
SW4637
SW4740
SW4839
SW5041

North Cornwall (Cornwall)

SW8470
SW8572
SW8573
SW8576
SW8676
SW8724
SW8972
SW8976
SW9170
SW9174
SW9178
SW9277
SW9280
SW9376
SW9380
SW9578
SW9579
SW9776
SW9780
SW9978
SX0080
SX0180
SX0382
SX0485
SX0488
SX0584
SX0588
SX0786
SX0988

The Lizard (Cornwall)

SW6523
SW6616
SW6620
SW6713
SW6717
SW6721
SW6911
SW6915
SW6919
SW6923
SW7113
SW7117
SW7121
SW7319
SW7323
SW7416
SW7517
SW7521
SW7719
SW7723
SW7816
SW7919
SW7921
SW7924
SW8121

APPENDIX III Analysis of sheep wool collected from the Chough nesting territories (*ca*.200g from each) in Wales during April 1989, and subjected to toxicological examination; ND = not detected; presence of Diazinon confirmed by mass spectrometry

Date	Source	Pesticides analysed for	
		Organochlorine	Organophosphorous
14th	Solva	ND	ND
15th	Cemaes	ND	ND
15th	Strumble (north)	ND	ND
15th	Strumble (south)	ND	154 ug/gm Diazinon
17th	Mwnt	ND	ND
17th	Bwlch Green (central Wales)	ND	ND

NOTE: Diazinon is used for the control of sheep scab.

Observations on two Red-billed Choughs *Pyrrhocorax pyrrhocorax* in Cornwall: habitat use and food intake

R.M. MEYER *Applied Ornithology Unit, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, UK*

The Chough has been extinct as a resident bird in Cornwall, and therefore England, since 1973. The arrival of 2 in Cornwall in 1986 offered a rare opportunity to acquire valuable information about the requirements and behaviour of Choughs at the most southerly extreme of their original English range. It was not possible to study them during the summer and autumn of 1986 due to their presence being unreported. The study describes the latter part of their stay in Cornwall for over 10 weeks from November 1986 to January 1987.

It is shown that sufficient elements of the Cornish countryside, particularly invertebrate food, exist to support Choughs but it cannot be claimed that this represents full long-term viability for breeding populations. The Choughs displayed good survival skills and coped well with adverse factors such as the agonistic attentions of Peregrines and larger corvids, and severe weather. Gapeworm infection was implicated in the death of one; the role of the earthworm both as a food source and, being a transport host of Gapeworm, as a potential danger is discussed.

The Chough is the rarest British crow. Unlike commoner species it is a specialist invertebrate feeder, often digging in the substrate for its food. It therefore requires a largely frost-free environment which, in Britain, restricts it to the coastline.[1] The last known sighting of a wild Chough in Cornwall was on 17 June 1973 (B. Boothby, pers. comm.), and it was believed at the time that this was the male of the last pair, its mate having died in 1968. The history of these last 'true' Cornish Choughs is not well documented, however. Subsequently, the autecology of the Chough has been studied in more detail, notably in N. Wales by Bullock[2] and Roberts[3,4] and in SW Scotland by Warnes.[5]

Due to the lack of published information on observations of wild Choughs in Cornwall, it would be valuable to have detailed descriptions of the activities of any birds seen in this area. In particular, there are virtually no data on the feeding behaviour of Choughs in Cornwall. Hence, the reported occurrence of two birds on the Rame peninsula west of Plymouth (Fig. 1) on 15 November 1986 presented an exceptional opportunity to examine the pioneering exploitation by Choughs of land at the very edge of their range.

The Choughs had apparently been resident on the peninsula in August, at least 15 weeks earlier, but this was not reported in ornithological circles. Consequently, this paper describes only the latter part of their stay in Cornwall, and discusses their feeding behaviour and ecological requirements up to their separate disappearances early in 1987. One bird, thought to be a female, developed respiratory distress, symptoms of Gapeworm *Syngamus trachea* infection, an impression reaffirmed by the discovery of the nematode eggs in the faeces of at least one of the Choughs.[6] It steadily lost condition until it disappeared (possibly killed by a Peregrine *Falco peregrinus*) on 4 January 1987. Earthworms (Lumbricidae) are transport hosts for Gapeworm,[7] and encysted larvae were found in earthworms from

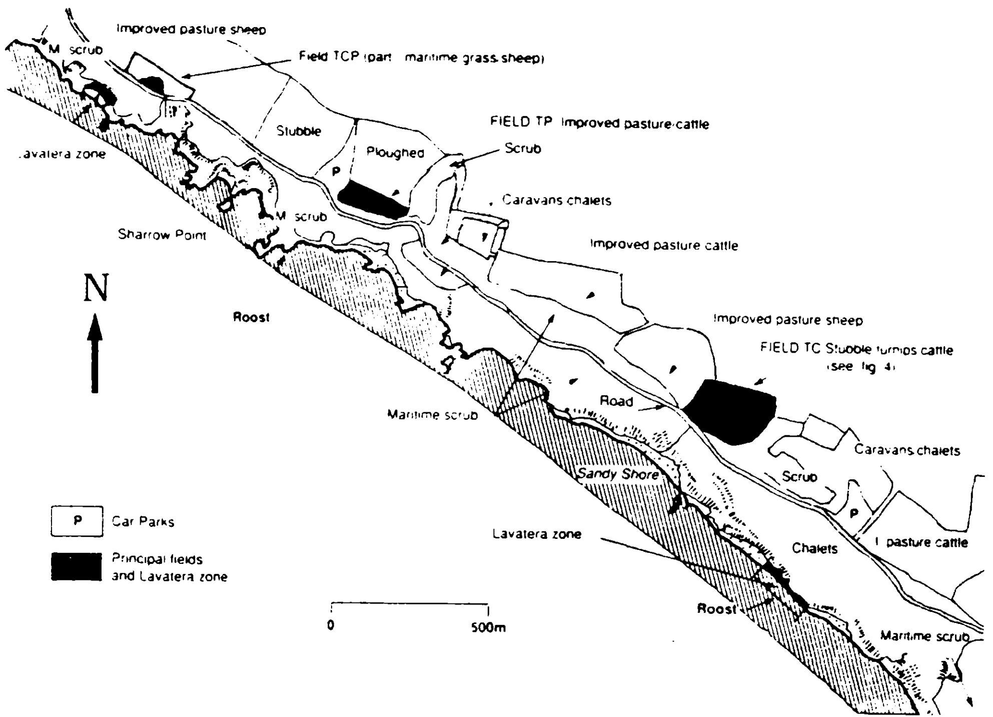
Improved pasture sheep
M scrub
Field TCP (part maritime grass sheep)
Stubble
FIELD TP Improved pasture cattle
Scrub
Lavatera zone
Ploughed
P
Caravans chalets
M scrub
Sharrow Point
Improved pasture cattle
N
Roost
Improved pasture sheep
FIELD TC Stubble turnips cattle (see fig 4)
Road
Maritime scrub
Caravans chalets
Sandy Shore
Scrub
P
Car Parks
Principal fields and Lavatera zone
Lavatera zone
Chalets
I pasture cattle
0
500m
Roost
Maritime scrub

Figure 2. The Rame study area.

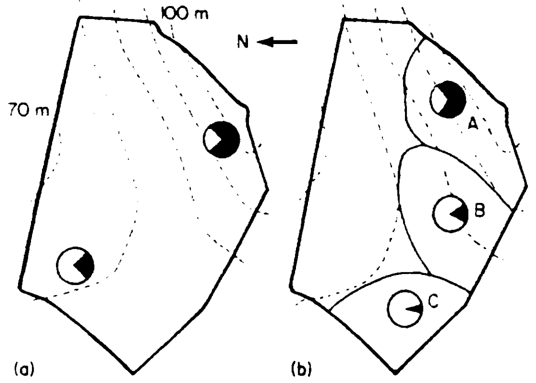
100 m
70 m
N
A
B
C
(a)
(b)

Figure 3. Invertebrate productivity (a) and Chough usage (b) in Field TC; contour interval 25 ft. Black segments represent indexes for productivity (soil samples and pit-fall recoveries combined—see Table 5) and usage. (a) Productivity: invertebrates recovered from pitfall traps: south used raised altitude section 0.19/trapnight (n = 340); north unused lower altitude section 0.16/trapnight (n = 275); and soil samples: used section 3.9/sample (n = 17); unused section 1.0/sample (n = 7). Overall productivity (black segments) 0.73 (used section) and 0.27 (unused section); Mann–Whitney U-test, U = 48, $P < 0.05$. N.B. Excludes fly larvae. Earthworms (used section 90.3%, unused section 9.7%) were a principal prey. (b) Usage by Choughs: proportions of feeding incidents in 3 clusters: A = 0.70, B = 0.175 and C = 0.125.

the birds had been seen foraging; a control set was located in a part of Field TC which was never seen to be used by the birds in 29 hr of observed presence nearby (see Fig. 3).

The second method sampled invertebrates in soil cores (80 mm diameter×80 mm). This method enabled spontaneous sampling in sites recently vacated by feeding birds. Results were compared with those from adjacent habitat, > 5 m away, which though apparently similar was not seen to be used. No site was seen to be used only once, most were visited repeatedly which gave ample opportunity to sample the resident prey spectrum without having to disturb the birds before the natural termination of a foraging bout.

Samples were, weather permitting, sorted immediately by hand. As a general rule, all organisms > 5 mm long were identified, at least to genus or family. The depth of the cores and their rapid extraction ensured that deep-burrowing earthworms were unlikely to be missed. The methods adopted were similar to those used by Bullock[2] and Warnes,[5] thus aiding comparison with their studies on Anglesey (N. Wales) and Islay (Inner Hebrides), respectively.

Chitinous and other durable remains of prey recovered from castings were identified with the aid of a ×12.5 binocular microscope (×15 with transmitted light was used for the recovery of earthworm chaetae). In all, 125 faecal samples and 42 pellets were collected for analysis. Later it became clear that a Kestrel *Falco tinnunculus* also used the roost. Consequently, 14 faecal and 30 pellet samples, including either vertebrate remains (bones or fur/feather) or collected from the ground below the Kestrel's perch were discarded even though most included earthworm and beetle remains and resembled the Choughs' castings in many respects. Beneath the roost, faeces could aggregate and lose integrity, thus making identification less exact.

Of the samples retained (111 faeces and 12 pellets), 75 (61%) were collected at the roost. The remainder—all faeces—were collected fresh from feeding sites.

RESULTS

Habitat selection

During 10 weeks from 19 November 1986 to 27 January 1987, 150 hr were spent on fieldwork. 85.7 hr were spent in pursuit of the birds. For 73.5 hr (85.7%) one or both could be accounted for. Both birds were alive for 70.9 hr (82.7%). During the time when both could be accounted for (60.5 hr), they showed great fidelity, being in contact for 56.4 hr (93.2%). Clearly, the birds influenced each other in their selection of foraging sites. However, of 15 days in which there was more than 90 min of pursuit data per day, the birds fed separately for part of at least 10, and habitat usage was established over 8008 'Chough minutes' (CMs, individuals×minutes observed) (Table 1). Habitat availability was calculated across the range plus a one field width border, as shown in Fig. 2.

The single most used site was Field TC (Fig. 2), situated on a steeply sloping hillside (*c*. 45°) and used for stubble-turnips – a variety of fast-growing brassica used as a stand-by forage crop for cattle in areas prone to drought and grass failure. Cattle had recently been removed from the field, and there was consequently much cow dung of various ages. This, in combination with the the large areas of bare stoney earth, was the main feeding area. The Choughs were often to be seen breaking open or turning over old dried cowpats, or probing fresher dung. Stones were frequently turned over and the birds also foraged beneath the Chickweed *Stellaria media* which covered the ground extensively. The birds would occasionally tug vigorously at the Chickweed in an attempt to remove it, at other times becoming entangled in it and tripping over.

Except for a week of sub-zero temperatures in mid-January when the ground was frozen to a depth of many centimetres (see below), and the surviving Chough (judged by its behaviour and slightly larger size to be male) spent its time exclusively on the cliffs, the birds were generally to be found visiting Field TC.

Table 1. Habitat selection and the estimated amount available within the Choughs observed range on the Rame peninsula, Cornwall, winter 1986–87

	Time spent in habitats		*Estimated available habitat*
Habitat	*CMs*	*%*	*(%)*
Cliffs without scrub	4123	51.4	8.9
Field TC: disturbed ground/abundant cattle dung	3058	38.1	3.3
Field TCP: unimproved turf/sheep dung	574	7.2	0.3
Field TP: improved pasture/less cattle dung	253	3.2	9.5
Walls, boundaries, scrub etc.	10	0.1	26.4
Cliffs with scrub or dwellings	0	0.0	25.7
Other agriculture: improved pasture/sheep and arable	0	0.0	25.9
Total	8008		

The most utilized habitat overall was the cliff region. The Rame peninsula is bio-climatically similar to other Chough and ex-Chough haunts in Britain. It has an annual average windspeed of > 6.6 m/s, which is characterized as 'very exposed, moderately warm and slightly moist', always with an absence of trees.[8]

Scrub and rank vegetation, which covers approximately 75% of the Rame cliffs (Table 1), is known to prevent Choughs from exploiting soil invertebrates even if they are present in good numbers,[9,10] and no feeding observations were recorded from this habitat at Rame. However, along the cliff-slopes there were many discrete pockets of therophytes, rock-heath and bare earth. During the severe weather of January, the surviving bird remained in excellent condition and was *never* seen away from a 150-m stretch of coast, which was also the main station for Tree Mallow *Lavatera arborea*. Fitter[11] shows the Tree Mallow as a Lusitanian species with a remarkably similar natural distribution in Britain and Ireland to the Chough; he also notes that occurrences elsewhere are likely to be escapes. At Rame, the substrate near the splash zone and beneath the broad Tree Mallow leaves remained friable during the freeze and rich in invertebrates, especially the woodlouse *Armadillidium vulgare*, millipedes (Diplopoda) and sandhoppers (Amphipoda).

Over half the observed feeding time at Rame occurred on scattered open cliff ground demonstrating that individual Choughs at least are able to find and successfully exploit pockets of suitable habitat.

Otherwise, during the study period the dung influenced habitats were a major resource. Although they were occupied for less than half the Choughs' active time, i.e. 3885 CMs (48.5%), compared with 4123 CMs on the cliffs (51.4%), they were foraged over more intensively: accounting for about 70% of actual feeding time.

The effects of sub-zero temperatures

Selection of habitat on days for which I had more than 90 min data for the birds is plotted proportionally in Fig. 4a. Frozen conditions in the agricultural fields concentrated activity on the cliff region, in particular the vicinity of the frost-sensitive *Lavatera* was described under Habitat selection. This produced a weak negative correlation in the relationship between temperature and habitat selection ($r_s = -0.295$) (Fig. 4b).

Habitat use

Resting and other sedentary behaviours were associated with non-agricultural habitats ($z = 3.74$, $P < 0.001$; see Table 2). Unless disturbed the birds seemed to leave the inland fields when they had consumed sufficient food. They also departed for special shelter crannies in heavy rain. Of 180.5 non-active CMs recorded (focal period+pursuit data), 177 (98%) were spent on the cliffs. Only on one occasion (3.5 min) was resting witnessed in agricultural habitats.

The birds were mobile for > 98% of daylight. During 159 separate periods of detailed focal sampling, amounting to 5.6 hr, various behaviours were recorded. Three-quarters of the samples (273 of 358 min; 76.3%) were collected from the agricultural fields, where, as has been shown, 70% of the feeding was done. These data were compared with those from the cliffs, where 85 min (23.7%) were obtained.

In one inquiry, amounting in all to > 3 hr, at least 60% of their time was spent actively foraging (i.e. with head down) (Table 3). Cattle dung on the improved pasture (Field TP) was used intensively (70%) but the birds were only seen in this field, which was near the main roosting site, at dawn and dusk. The semi-natural habitat (Field TCP) was used as intensively as the cliffs (65%). The large areas of bare stoney earth in Field TC caused more varied feeding behaviour and evidently yielded sufficient rewards: in 120 min of observations on 10 December, 346 food items were seen to be taken ($\bar{x} = 1/20.7$ s; sd 17.2 s; range 12.0–65.0 s) by one or other of the pair.

As is shown in Table 3, there was no significant difference between the two primary habitats in foraging intensity. When ground movement is regarded as an essential component of foraging behaviour (i.e. hunting), significant differences are found (Table 2, $P < 0.01$).

In respect of actual 'head down' foraging time, the difference between the two habitats was not significant at the 5% level ($z = 1.31$), therefore the nutritional rewards afforded by

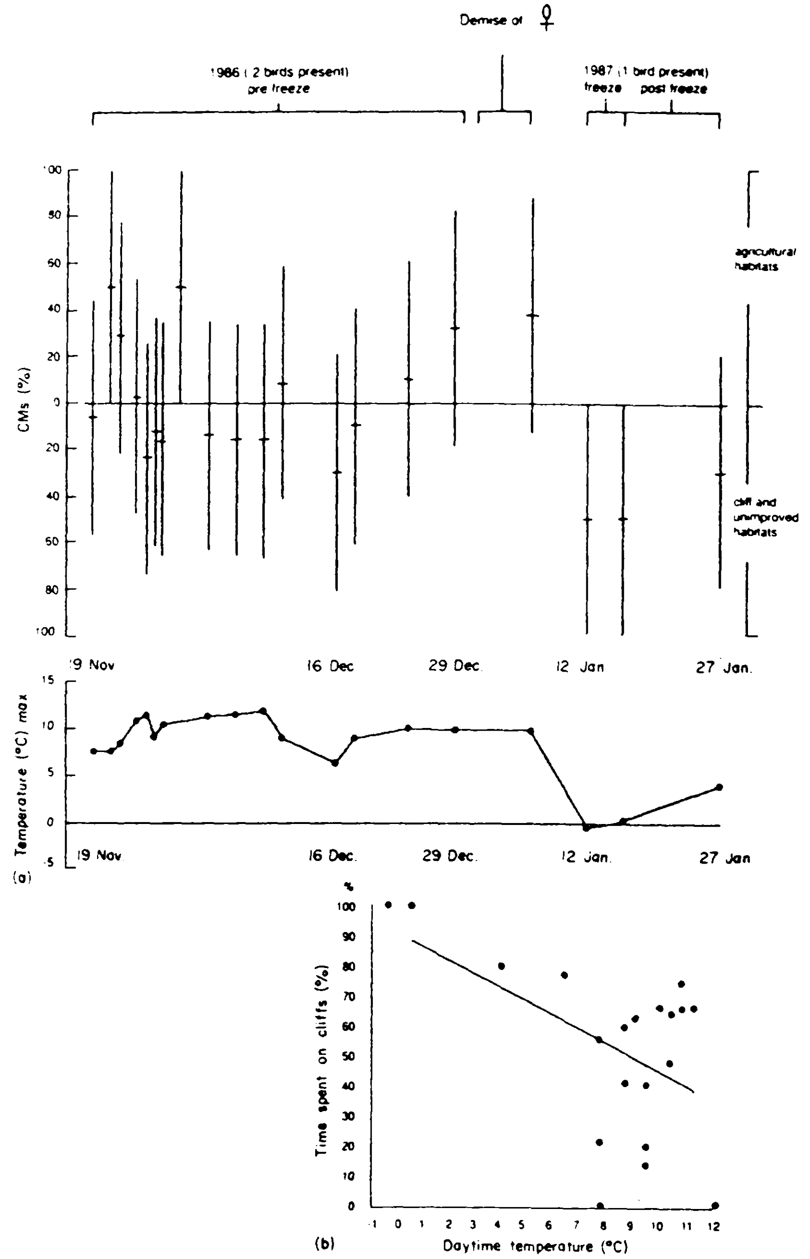

Figure 4. (a) Habitat selection by Choughs on the Rame peninsula, Cornwall, from 19 November 1986 to 27 January 1987, shown proportionally by percentage bands, with means indicated by cross bars, over corresponding maximum daytime temperatures, (b) percentage of time spent on cliffs plotted against temperature, r_s = 0.295.

the agricultural habitats, at least during winter, would appear to be even more important. In the only other habitat with reasonable data, a mean rate of 4.1 swallows/bird/minute (n = 9.5 m) was found; during foraging time, success was 9.1 s/b/m (n = 4.8 m).

Diet and food availability

Difficulty was experienced in recovering fly (Diptera) larval remains from faecal samples, otherwise the available prey spectrum, as suggested by pitfall trapping and soil sampling, matched the principal prey items as shown by faecal and pellet analysis (Table 4a) quite closely. Earthworms and beetles (mainly adults as shown in Table 4c) were the most important foods: remains of both appearing in well over half the samples. By use of a ×60 telescope, earthworms could often be seen to be taken, especially from Field TC.

Background sampling (Table 5) suggests the

Table 2. Hunting time (foraging+integral movements between foraging patches) and non-hunting time, mainly vigilance. Field TC was the most intensively used for hunting, $z = 2.68$, $P < 0.01$, and the cliffs were the most used for other activities, $z = 3.74$, $P < 0.001$. Mann–Whitney *U*-test, *z* statistic

	Apportionment of focal period time spent hunting (foraging+searching) and not hunting					
	Focal periods		*Hunting time*		*Not hunting*	
Habitat	$\bar{x}$	*n*	$\bar{x}$	(%)	$\bar{x}$	(%)
Field TC	57.7	73	45.5	79**	12.1	21
Cliffs	58.1	42	39.5	68	18.6	32***

Table 3. Time spent foraging (excluding vigilance and other integral behaviours) in the main agricultural (Field TC) and non-agricultural (cliffs) habitats expressed as percentages of complete focal periods. Head down behaviour did not differ significantly between the two habitats ($z = 1.31$; $P > 0.05$, Mann–Whitney *U*-test, *z* statistic for large samples

	Distribution of focal periods		*Distribution of foraging bouts*	
Habitat	$\bar{x}$	*n*	$\bar{x}$	(%)
Agricultural	57.7	73	34.4	60
Non-agricultural	60.5	45	39.1	65
Total	58.8	118	36.2	62

importance of dung and of the cliffs as resources. The most frequent taxa recovered, depending on the method of sampling, were earthworms, beetles and fly larvae. Cliffs, though accommodating a more diverse fauna, were less productive than the dung influenced habitats.

On a specific level, woodlice, *Armadillidium vulgare, Philoscia muscorum* and *Metoponorthus cingendus*, were frequently recovered from cliff feeding-sites, as were, during the sub-zero period, the larvae of the St Mark's fly *Bibio marci* from patches of exposed friable earth near vegetation. In the fields, larvae of the dipteran families Scatophagidae, Anisopodidae, Muscidae and Calliphoridae were common in cow dung in which the Choughs were feeding. Spiders (Aranaea) were regularly recovered from pitfall traps. Evidence of ants (Formicoidea) was widespread but they were seldom seen due to the season.

Earthworms, mainly *Lumbricus rubellus, Allolobophora chlorotica* and *Eisenia fetida*, were plentiful in dung influenced habitats: and were recovered at the rate of 2.5 per soil sample from fields TC, TP and TCP combined. By comparison, on the cliffs, only one earthworm was found in 20 samples. Beetles (adults and larvae) also were abundant: ground beetles (Carabidae), rove beetles (Staphylinidae), dung beetles (Scarabaeidae and Geotrupidae), darkling or false rove beetles (Tenebrionidae) and click beetles (Elateridae) were all represented. Notable genera, as shown by faecal samples, were *Aphodius, Opatrum, Amara, Geotrupes* and *Agriotes;* these were also well represented in background samples, as was the genus *Harpalus*.

Table 4. (a) Percentage frequency of food remains in faecal and pellet castings of Choughs on the Rame peninsula, Cornwall, winter 1986–87; (b) proportions of beetle (Coleoptera) taxa; and (c) proportions of beetle age-classes

Taxon	*Faeces*	*Pellets*	*Total*
(a) Percentage of castings containing food remains			
Earthworms	74.8	38.5	70.7
Coleoptera (all ages)	55.3	76.9	57.8
Flies (all ages)	27.2	0	24.1
Seeds	6.8	6.9	6.9
Earwigs (Dermaptera)	5.8	7.1	6.0
Ants	1.9	7.7	2.6
Lepidoptera (larvae)	0	23.1	2.6
Spiders	1.0	7.1	1.7
Millipedes (Diplopoda)	1.9	0	1.7
Sample sizes	103	13	116
(b) Proportions of Coleoptera taxa (all ages) in diet			
Scarabs/*Geotrupes* sp.	0.32	0.50	0.36
Carabidae	0.34	0.22	0.32
Tenebrionidae	0.19	0.06	0.17
Curculionidae	0	0.11	0.02
indeterminates	0.14	0.11	0.14
(c) Proportions of Coleoptera adults and larvae in diet			
Adults	0.97	0.75	0.94
Larvae	0.03	0.25	0.06

Foraging success

Foraging success, identified by pecks which were followed by mandibulation and swallowing of prey items, is shown in Table 6. Good visibility was not always possible, so the most accurate counts in the two principle habitats were used. Over all focal time, the cliffs afforded a significantly better success rate ($P < 0.05$) within a wide variance. However, allowance should be made for the varying sizes and therefore different nutritional rewards per prey item. Earthworms, which were commonly seen to be taken from the agricultural fields (see Diet and food availability, and Table 5), can weigh several grams while the arthropod prey rarely exceeded 1 g. Measured calorifically, earthworms give 20.0 J/mg (only slightly less than beetle (Coleoptera) larvae at 23.4 J/mg)[12] and, of course, can sustain large vertebrate species such as the Badger *Meles meles*.[13]

Inter-specific interactions

Interactions with other species occurred in all habitats but Choughs were not seen to feed in association with other corvids except that Magpies *Pica pica* were often close by. Waite[14] found significant behavioural resource partitioning between sympatric Carrion Crows *Corvus corone*, Rooks *C. frugilegus* and Jackdaws *C. monedula* but no unique niche for the Magpie. A Peregrine was twice seen to stoop at the Choughs, once in Field TC (only one Chough present) and once on the cliffs (both present). Other agonistic interactions were observed between Ravens *C. corax*, Carrion Crows, Rooks and Jackdaws. Rooks elicited an agonistic response only when the two were < 2 m apart. Jackdaws were either ignored or chased away. Only one serious 'dog-fight' with Jackdaws was observed, at a pre-roost encounter, and the Choughs had no trouble in emerging victorious. Visible Raven

Table 5. Abundancies of potential prey as shown by soil-sampling (average frequency per sample) and pit-fall trapping (% recovery/total trap nights) on the Rame peninsula, Cornwall, winter 1986–87

	Soil Samples					*Pit-falls*				
	Fields				*Cliffs*	*Fields*				*Cliffs*
	TC		*TP*	*TCP*		*TC*		*TP*	*TCP*	
Potential prey	*Used*	*Unused*				*Used*	*Unused*			
Beetles (all ages)	0.4	0.3	0.3	1.0	0.3	17.9	15.3	13.5	7.7	5.0
[Beetle adults	0.35	0	0.2	0.3	0.25	4.1	5.8	3.0	4.4	1.2]
[Beetle larvae	0.1	0.3	0.1	0.7	0.05	13.8	9.4	10.5	3.2	3.8]
Earthworms	2.8	0.9	3.4	1.3	0.05	0	0	0	0	0.3
Flies	1.65	0.3	0	2.0	1.0	0	0	0	0	1.2
Spiders	0.4	0	0	0	0.05	0.9	0.4	2.7	1.6	1.8
Woodlice (Isopoda)	0	0	0	0	1.75	0.3	0	0.9	0.8	2.1
Enchytraeids	0.1	0	0.1	0.7	1.2	0	0	0	0	0
Ants	0	0	0	0	0.8	0	0	0	0	0.6
Molluscs	0	0	0	0	0.35	0	0	0	0	0.9
Millipedes	0	0	0	0	0.2	0	0	0	0	1.5
Centipedes	0	0	0	0	0.05	0	0	0	0	0
Amphipods	0	0	0	0	0.05	0	0	0	0	0.6
Lepidoptera larvae	0	0	0	0	0	0	0.4	0	0	1.2
	No. soil samples					*No. trap-nights*				
Sample sizes	17	7	9	3	20	340	275	332	248	338

Table 6. Foraging success in the principal habitats. Successful pecks/bird/minute (s/b/m) ±1 se during focal period minutes (accurate counts only included)

	s/b/m rate					
	Foraging time			*All time*		
Habitat	$\bar{x}$	*se*	*min*	$\bar{x}$	*se*	*min*
Field TC	7.4	5.3	59.0	4.0	3.1	245.3
Cliffs	12.8	13.1	11.9	7.2*	7.9	20.9

$^*P < 0.05$; $z = 2.28$, Mann–Whitney *U*-test, *z* statistic.

and Carrion Crow presence always caused anxiety. Subsequent observations in West Wales indicate that agonistic actions by these two corvids towards Choughs occur mainly in the winter (R.M. Meyer, unpublished data), and Waite[15] has suggested that such aggression is not in response to food competition but against birds whose foraging behaviour reduced the availability of earthworms to the Carrion Crows.

DISCUSSION

The short duration of this study cannot, of itself, indicate whether Cornwall is still capable of supporting wild Choughs. It is known that the birds under observation were present on the Rame peninsula from at least high summer until deep winter; a period which included a fairly typical range of weather conditions with a spell of severe sub-zero temperatures.

It is possible that the birds were not as experienced or as adept at feeding profitably as birds within their stronghold region in Britain, and were feeding more randomly (D.B.A. Thompson, pers. comm.). However, the eventual unfortunate demise of one bird (thought to be female), almost certainly due to Gapeworm infection, and the possibly consequential emigration of its mate, perhaps should not be taken as conclusive evidence of unsuitability either. It has been shown that Gapeworm is endemic in many wild bird species,[6,7] and birds in a pioneering situation might be at a raised level of susceptibility due to increased stress and reduced immunity; inexperience might also render them less able to differentiate between infected and non-infected prey when feeding, as suggested by Thompson,[16] and Brown and Thompson.[17] Gapeworm in Choughs is discussed more fully by Bignal *et al.*,[18] and Meyer and Simpson.[6]

Until the final phase, the Choughs were together for more than 90% of the time and appeared to be a compatible pair. Until the illness of one became debilitating, there were no apparent feeding or survival difficulties.

Active time was fairly equally divided between the cliffs and agricultural fields. One field (TC), down to brassicas but with large amounts of bovine dung and bare earth, was the most used single site. It is very evident from these data that the majority of land within the range being exploited by the birds was of little value to them: an area of about 87.5% accommodating the birds for only 3.3% of the time.

In Field TC, earthworms were a common prey. Subsequent work has demonstrated that earthworms are also frequently taken by Choughs in Pembrokeshire, West Wales. During one year, in 4 separate study areas, earthworm remains featured in 21.4% of faecal samples ($n = 250$); during the winter, possibly when other invertebrate food is less plentiful, the frequency increased to 35.9% ($n = 109$).[19] In previous studies,[2,3,5] all carried out farther north, such a dependence has not been shown, although it is possible that earthworm chaetae have been overlooked in faecal analysis. The earthworm could, therefore, be something of a two-edged sword: a vital food resource, especially in the winter, where Choughs rely on rough pasture and other dung-influenced habitats, but a serious life risk to stressed and inexperienced birds.

The Choughs were efficient in selecting productive foraging areas, and able to switch as conditions dictated. Diptera larvae were possibly equally important as a dietary component and were far more frequent than beetles in soil samples; like earthworms and cranefly (Tipulidae) larvae, they are, of course, unlikely to appear in pitfall traps, and their dietary importance is almost certainly under-represented. Tipulids were seen to be taken but are mostly utilized by Choughs during the summer months, when the larvae are fully grown.[2]

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APPENDIX V Report of study trip to Ramsey Island in July 1989. (Updated from Meyer 1989c)

INTRODUCTION/AIMS

Ramsey Island is an important centre for the Chough in Wales (Donovan 1972, and Bullock *et al.* 1985). This is a summary of 3 days spent on the island in July 1989. It includes indications of the Chough's diet and habitat selection. The weather was very hot, and the preceding months had been some of the dryest on record. This was reflected in the vegetation, which in turn probably influenced the results.

The aims of this short study were:

1. To assess the post-fledging behaviour and diet.
2. To complement a similar earlier exercise (Cowdy 1972).
3. To enable the habits of island Choughs to be related to mainland Choughs.

METHODS

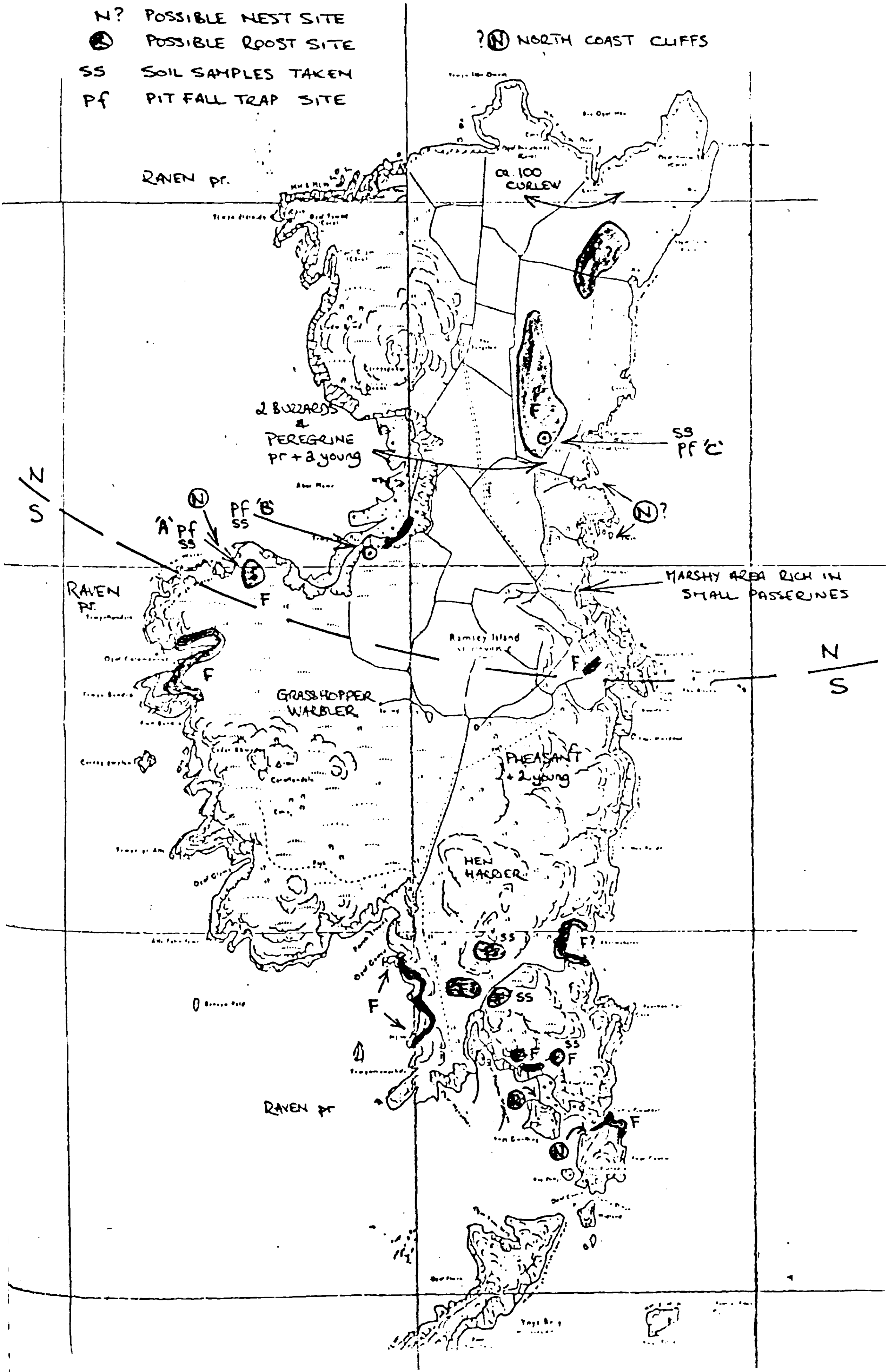
The northern and southern parts of the island were searched on separate days for evidence of Choughs. When found they were observed by telescope, and their behaviour and habitat selection noted and marked on maps. Periods in each habitat were timed, and after the birds' departure, investigations were made, by soil sampling and faecal collection, into their diet. Note was also taken of the general vegetation; soil cores measured 100x80mm.

Pitfall trapping was carried out in 3 habitat categories. Additional information of the prey spectrum was obtained by pitfall trapping: 3 sets of 5 plastic vending cups were positioned where shown in Fig 1., and as described in Chapter 2. They were in place for 2 days and 2 nights, and in order to make the results more meaningful to Chough ecology, they were emptied at dawn and dusk to entail separation of day- and night-active taxa (see Addendum).

Virtually all observations were of feeding birds, therefore usage is quantified by multiplying the number of minutes observed feeding by the number of Choughs present (excluding juveniles, which were neither selecting habitats nor feeding independently) to give Feeding Chough Minutes (FCMs).

RAMSEY ISLAND: CHOUGH OCCU[illegible]CES & SELECTED ADDITIONAL BIRD NOTES - JUNE 1989

● FEEDING AREA
F? PROBABLE FEEDING AREA
Ⓝ PROBABLE NEST SITE
N? POSSIBLE NEST SITE
Ⓡ POSSIBLE ROOST SITE
SS SOIL SAMPLES TAKEN
pf PIT FALL TRAP SITE


?Ⓝ NORTH COAST CLIFFS
RAVEN pr.
ca. 100 CURLEW
2 BUZZARDS & PEREGRINE pr + 2 young
SS pf 'C'
F
Ⓝ?
Ⓝ
pf 'B' SS
'A' pf SS
N/S
RAVEN pr.
F
MARSHY AREA RICH IN SMALL PASSERINES
Ramsey Island
N/S
F
GRASSHOPPER WARBLER
PHEASANT + 2 young
HEN HARRIER
SS
F?
SS
F
SS F
Ⓡ
F
Ⓝ
RAVEN pr

RESULTS AND DISCUSSIONS

Effort

30.3 hours were spent in the field. Interestingly, virtually a third was spent in each of three occupations: searching (10.3hrs), observing (9.9hrs) and sampling diet and invertebrates (10.1hrs), but time spent in profitless searching decreased dramatically from 66% to 15% over the 3 days.

Numbers

The maximum number of Choughs seen at any one time was 11. Historically, much larger numbers have been recorded (Donovan 1972). A breeding population of between 3 and 5 pairs was estimated. This is the level estimated for the island during periods of low grazing pressure (Bullock *et al.* 1985). Few young birds were seen, with only 2 or 3 family parties, each with only one or two young. Several apparently well-mated pairs were observed without young.

About two weeks earlier, J.W. Donovan recorded and photographed one family with 4 young. It is possible that the drought adversely affected foraging success and consequently the health of juveniles, making them easier prey for Peregrines *Falco peregrinus*, of which one pair is known to have nested successfully on Ramsey in 1989. P. Taylor relates personal and third party accounts of Peregrines pursuing Choughs during 1989 at and near Camaes Head. Elsewhere in Pembrokeshire, evidence, albeit of a sketchy nature, also suggests low productivity in Choughs.

Habitat usage

Four main habitats were used:

1. Unimproved maritime grassland, heavily grazed by the 3 main herbivores on the island: rabbits of which many thousands exist (Cowdy 1972); *ca*.250 sheep; and *ca*.45 Red deer. Such grazing coupled to the drought resulted in a sparse vegetation, which, while giving access to the substrate for the probing and digging of Choughs, also made feeding difficult and soil invertebrates scarce.
2. Old burnt heath, Erratic burning has resulted in compartments of land at different stages of regeneration. These appear to be important to the Choughs.
3. Drought affected hollows (with Marsh pennywort *Hydrocotyle vulgaris* and Silverweed *Potentilla anserina*), with less dry substrate still supporting eathworms and tipulid larvae (leatherjackets).
4. Clifflands.

Table 1 Habitat usage: minutes x no. of feeding Choughs (FCMs)

Habitat	FCMs	%	No. events
Maritime grassland, heavily grazed	1538	69.5	10
Old burntheath with bare earth and regeneration	252	11.4	8
Damp hollow	207	9.4	6
Cliffs	198	8.9	28
Other	19	0.9	3
Total	2214		51

Results are summarised in Table 1.

The cliffs were visited most frequently but stays were shorter, averaging only about 7mins, compared to 2.5 hours during one morning on grazed old pasture, and periods of ca..05hr each on heath and in the damp hollow. Only in the latter were earthworms found.

Donovan (1972) suggested the importance of sheep grazing on Ramsay (comparing it with Skomer), and subsequently this has been confirmed, notably on the Calf of Man by Bullock & del-Nevo (1983) and in review by Bullock *et al.* (1985) for Bardsey and Ramsey islands.

Diet

The frequency of prey remains from faecal analysis is given in Table 5.17. Adult beetles were represented in all bar one of 49 samples, dung beetles (Scarabaeidae) were in nearly 80%, but this was not corroborated by invertebrate sampling at feeding sites, thus highlighting discrepancies between feeding observations, invertebrate sampling and feacal evidence. This could be corrected with more effort. There are 3 possible explanations: a) the birds were feeding in island habitats not identified; b) sampling techniques were inadequate; and c) the birds were feeding in mainland sites. The latter seems most likely since flights across Ramsey Sound are frequent. *Aphodius* beetles, possibly *A. rufipes*, were an important component.

The ant component, though low (8%), was supplemented by *Lasius alienus* a rather mobile heathland species (Brian 1977); 2 individuals were alates. The large ground beetle *Abax parallelopipedus* is normally regarded as a woodland species (Lindroth 1973), although one specimen was been found beneath a stone in open mountain heath on the summit of Ben Mhor, S Uist (P. Buckland pers. comm.). The most frequent insect in the pellets was a chafer beetle, *Amphimallon solstitialis/ochraceus*). It proved impossible to separate these species on the pellet fragments; both are largely coastal and restricted to southern England and Wales, the latter species being rarer. *A. solstitialis* is a pest of arable and grassland, although use of agri-chemicals has led to its progressive restriction to areas of old grassland (*ibid.*). The numbers of chafers here is a reflection of the study being undertaken at the time of peak emergence of adult chafers in one of the few remaining optimal habitats for this species.

Table 2 Frequency (%) of invertebrates in soil cores. Col = Coleoptera (beetles); Dip = Diptera (flys); Spi = spiders; Ewm = Earthworms; Wl = Woodlice; Cen = centipedes; Mil = millipedes; -ve = nothing found

		% Presence score/sample								
Site	n	Col	Dip	Ants	Spi	Ewm	Wl	Cen	Mil	-ve
Feeding	26	23.1	46.2	30.8	30.8	11.6	3.8	3.8	3.8	19.2
Non-feeding	10	10.0	28.0	20.0	0	0	10.0	20.0	0	50.0
Total	36	19.4	38.9	27.8	22.2	8.3	5.55	8.3	2.8	27.8

Table 3 Frequency of invertebrates/food units recovered from pitfall traps;
B = Beetles; BL = Beetle larvae; EW = Earwigs; A = Ants; WL = Woodlice; F= Flys; H = Hermiptera (bugs); S = Spiders; M = Moths; O = Other

		Prey taxa Individuals/food units										
Site catch	Trap minutes	B	BL	EW	A	WL	F	H	S	N	O	Total
A Day	6615	2/2	0	0	1/1	0	12/14	53/53	1/1	2/2	0	71/73
Night	4610	8/12	0	1/1	0	0	7/7	4/4	4/6	0	0	25/31
Total	11225	10/14	0	1/1	1/1	0	19/21	57/57	5/7	2/2	0	96/104
B Day	6835	2/6	0	0	23/23	0	2/2	7/7	1/1	1/1	1/1	37/41
Night	4640	9/26	1/2	0	7/7	2/2	1/1	2/2	1/1	1/1	0	24/42
Total	11475	11/32	1/2	0	30/30	2/2	3/3	9/9	2/2	2/2	1/1	61/83
C Day	5050	0	0	0	2/2	0	13/14	10/10	5/7	0	0	30/33
Night	4935	2/3	0	0	8/8	0	0	4/4	1/1	0	0	15/16
Total	9985	2/3	0	0	10/10	0	13/14	14/14	6/8	0	0	45/49

Site key (see map for location)
A = Old burnt heath (Chough feeding area);
B = Rabbit grazed maritime grass;
C = Sheep grazed maritime grass (Chough feeding area)

The results of soil sampling are summarised in Table 2. The beetle tally from the feeding sites was equally divided between adults and larvae but only one scarab beetle (a larva) was found. The abundance of invertebrates in feeding habitats (1.5 per sample) was almost double that in the unused areas (0.8). The results of pitfall trapping are summarised in Table 3 and give a measure of relative productivity. In order to make the results more meaningful to Chough ecology, traps were emptied at dawn and dusk to differentiate between day- and night-active prey (Addendum). Individual invertebrates (of varying size) were converted to 'food units': 1 =small (eg. ant-sized, <5 x 2mm); 2 = medium (eg. earwig-sized, 5 x 2mm - 10 x 4mm); 3 = (eg. large beetle >10 x 4mm). Hanbury (1975) undertook a larger scale invertebrate sampling programme on the island.

SUMMARY

The brief term of this study allows only a fascinating glimpse into the ecology of the Chough on Ramsey. Nevertheless, the importance of herbivores (rabbits, sheep and deer - probably in that order) and the consequent good heart of the grassland, despite the parched conditions, is 'inescapable', as Bullock and del-Nevo (1983) decided for Choughs generally. On Ramsey, the Red deer, in breaking through ranker growth, creating poached areas and diversifying the invertebrate fauna might fulfill the role of cattle elsewhere. The high numbers of rabbits are clearly a very beneficial force and should be encouraged at all costs unless numbers of sheep can be significantly increased. The grazing of cliffslopes where they occur and clifftop zones should similarly be encouraged.

The areas of old burnt heath provide a valuable resource, and judicious 'cool' swaling should certainly be considered as a valid on-going management ploy to create open areas and expose the substrate. Other methods of scarifying could also be considered.

Adult beetles (especially Scarabaeids) are the most important single taxon in their diet, as on the adjacent mainland (Meyer 1989).

A major advantage of Ramsey is its seclusion and freedom from casual (yet often persistent) human disturbance such as picnicking, sightseeing, walking, bird-watching, climbing etc., and this should be preserved at all costs although by no means need this curtail legitimate usage, eg. farming, carefully controlled holiday trade and field-study exploits.

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REFERENCES See main bibliography

ADDENDUM Day and night catches of prey in pitfall traps

The species of the principal taxa from Table 4 are given below in more detail. A chi-square test (Yates' correction) was done on the diurnality (D) and nocturnality (N) of each catch. All sites were located in Chough feeding habitats.

Total

Beetles Predominantly nocturnal; all adults except 'L'.

D: indet. sp. 2,
Carabidae sp. 1, *Pterostichus madidus* 1 — 4

N: Carabidae sp. 1, *P. madidus* 10, *Calathus ambiguus* 1,
Staphylinidae sp. 1, *Ocypus* (L) 1,
Leiodidae sp. 1,
Curculionidae
Otiorhynchus rugostriatus 2, *Alophus triguttatus* 1,
indet. sp. 2 — 20

$X^2_1 = 9.38$, $P<0.01$

Ants Predominantly diurnally surface active.

D: *Myrmica scabrinodis* 25, *Lasius flavus* 1, — 26

N: *M. scabrinodis* 11, *L. flavus* 4, — 15

$X^2_1 = 2.44$, N.S.

Flys Predominantly diurnal; all imagines

D: Brachycera Dolichopodidae 11
Cyclorrhapha Muscidae 4, Fanniidae 3, Tachinidae 2,
Phoridae 7 — 27

N: Brachycera Dolichopodidae 6
Cyclorrhapha Anthomyiidae 1
indet. sp. 1 — 8

$X^2_1 = 9.26$, $P<0.01$

Spiders

D: *Pardosa* sp. 4, *P. agrestis* 1, *P. pullata* 1, Gnaphosidae 1 — 7

N: *Trochosa terricola* 1, *Haplodrassus* sp. 1, Gnaphosidae 1,
Linyphiidae 1
Phalangium opilio 1
indet. sp. 1 — 6

$X^2_1 = 0.00$, N.S.

The most surprising aspect of the above small experiment is the very high degree of nocturnality in the beetle assemblage ($P<0.01$): the most important prey resource overall for Choughs. Fly larvae, more likely prey for Choughs than the adults caught, were unrecorded and less likely to be by pitfall trapping, as were other principal prey categories, *e.g.* earthworms and leatherjackets.

Appendix VI Numbers of Choughs recorded on Skomer Island, principally from 1962 1988. Data collected from observatory records (data from 1975 and 1976 missing)

Table 1 No. observation days/no. recorded days Choughs seen

	Year 19..												
Month	62	63	64	65	66	67	68	69	70	71	72	73	74
Feb	0/0	1/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Mar	2/?	?/15	27/?	20/?	26/?	26/17	0/0	16/6	4/3	28/11	16/9	7/6	19/6
Apr	24/?	19/2	27/?	30/?	29/?	28/22	27/12	30/8	30/11	30/14	30/6	30/2	10/7
May	30/?	28/?	30/?	30/?	31/?	31/14	31/6	31/5	31/11	31/5	31/2	31/?	?/3
Jun	29/?	24/?	30/?	30/?	30/27	30/8	27/?	30/9	30/8	30/11	30/?	30/?	24/6
Jly	25/?	18/?	31/?	31/?	31/17	31/6	31/?	21/9	31/9	20/8	31/3	31/4	1/1
Aug	17/?	20/?	31/?	31/?	31/27	31/11	6/3	31/8	31/8	18/11	31/5	31/?	14/1
Sep	30/?	22/?	27/?	23/?	30/28	30/14	9/9	13/3	30/12	30/24	30/8	17/9	10/1
Oct	28/?	13/?	31/?	16/?	15/13	30/7	?/14	0/0	10/1	8/4	5/4	10/10	12/1

Month	77	78	79	80	81	82	83	84	85	86	87	88
Jan	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	21/?	0/0	0/0	0/0
Feb	0/0	0/0	0/0	0/0	0/0	0/0	0/0	2/0	8/0	0/0	0/0	0/0
Mar	10/5	30/3	21/1	7/7	3/3	20/20	31/8	31/1	31/1	24/21	21/20	26/21
Apr	30/3	30/8	30/6	27/14	13/13	28/18	30/?	30/11	30/3	30/21	30/16	30/3
May	30/?	31/?	31/?	31/?	17/17	31/?	31/?	31/2	31/6	31/4	31/?	31/?
Jun	30/2	30/?	30/?	30/?	26/4	30/?	30/?	30/?	30/5	30/?	30/?	30/?
Jly	31/?	31/?	3/?	31/?	31/?	31/?	31/?	31/?	31/9	31/2	31/1	31/11
Aug	31/?	31/1	18/18	4/4	31/?	31/?	22/15	31/?	31/9	31/2	31/?	20/15
Sep	30/?	30/?	12/12	13/13	30/?	29/1	30/19	30/?	30/5	30/22	25/22	24/23
Oct	26/1	15/2	25/1	13/13	26/3	31/1	31/18	30/1	31/?	20/20	8/7	18/18
Nov	0/0	0/0	0/0	13/13	0/0	7/?	30/17	30/?	30/?	12/12	3/3	0/0
Dec	0/0	0/0	0/0	5/5	0/0	0/0	10/?	31/?	12/?	0/0	3/3	0/0

Table 2 Aggregate total recorded/maximum recorded flock size

	Year 19..								
Month	62	63	64	65	66	67	68	69	70
Feb	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Mar	-/-	35/-	91/10	50/7	120/13	76/8	-/-	16/6	8/3
Apr	-/-	7/5	68/5	78/7	92/9	66/7	57/6+	20/4	30/6
May	-/-	-/-	76/5	67/5	117/9	33/4	34/6	19/4	30/6
Jun	-/-	-/-	-/-	112/8	75/4	34/9	-/-	26/5	22/4
Jly	-/-	-/-	?19/12	126/8	61/9	22/5	-/-	20/5	36/7
Aug	?/9	?/4	?/9	116/10	88/10	46/12	7/3	28/5	27/6
Sep	-/-	78/9	?/7	66/6	83/7	38/7	41/6	8/4	35/9
Oct	?26/12	?21/11	?/15	42/5	31/4	15/3	37/5	-/-	2/2

Month	77	78	79	80	81	82	83	84	85
Jan	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-
Feb	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-
Mar	25/6	15/7	7/1	22/6	7/3	56/6	46/6	4/1	6/1
Apr	12/4	43/6	41/10	39/6	21/2	42/4	-/-	64/8	18/7
May	-/-	-/-	-/-	-/-	26/2	-/-	-/-	11/6	31/6
Jun	14/7	-/-	-/-	-/-	5/2	-/-	-/-	-/-	26/7
Jly	-/-	?/6	-/-	-/-	-/-	-/-	-/-	-/-	64/13
Aug	-/-	?16/1	58/8	16/8	-/-	-/-	29/2	-/-	46/30
Sep	-/-	-/-	33/6	50/7	-/-	?6/1	43/6	?/10	85/25
Oct	?8/1	22/?	7/1	35/6	12/6	?6/1	62/6	?6/1	-/-
Nov	-/-	-/-	-/-	32/6	-/-	-/-	50/6	-/-	-/-
Dec	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-

Table 3 Breeding success of Choughs on Skomer Island (available data)

Year	No. pairs breeding + young produced (and comments)
1946	2, possibly 3 pairs bred
1960	1 + 1
1961	1 + 4
1962	2 + 6
1963	0
1964	2 + 5
1965	2 + 3
1966	2 + 2 (1 pair failed)
1967	1 + 3 (possibly 2nd pair)
1968	1 + 3
1969	2 + 4
1970	2 + ?
1971	2 + ? (both fledged young)
1972	2 + 5
1973	3 + 8
1974	0
1975	1 + 0
1976	0
1977	?
1978	?
1979	?
1980	0
1981	1 + 2
1982	1 + ?
1983	2 + 2 (1 pair failed)
1984	2 + ? (1 pair fledged young)
1985	2, possibly 3 pairs bred
1986	3 + 10 (possibly 4th pair)
1987	3 + 5-8 (possibly 4th pair)
1988	1 + 1

Gapeworm infection in Choughs *Pyrrhocorax pyrrhocorax*: further evidence

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VIC R. SIMPSON, *Chacewater, Truro, Cornwall, UK*

Gapeworm infection is familiar in a variety of species in captivity but little is known about the effects of such diseases on wild populations. The present note provides further information on Gapeworm in both wild and captive Choughs in Cornwall, and discusses its possible inhibitory effects on birds pioneering new or strange habitats. The disease is implicated in the death of one of two Choughs to return to Cornwall after an absence of over 10 years.

In a recent issue of Ringing and Migration, Bignal *et al.*[1] described the occurrence of Gapeworms *Syngamus trachea* in free-living Choughs *Pyrrhocorax pyrrhocorax* on the island of Islay off the western coast of Scotland. They noted that the condition had previously been recorded in Choughs on the Calf of Man,[2] and suggested possible effects of chronic infestations on relatively small and isolated populations of Choughs. This short note describes infection in captive and free-flying Choughs in Cornwall.

Syngamus trachea is a blood-sucking nematode that infects the trachea of many species of birds. The worms live in a state of permanent copulation, and the female produces characteristic eggs with caps at both ends (bipolar). The worms cause considerable irritation to the lining of the trachea and, if significant numbers are present, also obstruct the airways. Coughed-up eggs are swallowed and appear in the birds' droppings. The eggs hatch to produce larvae which may be ingested by invertebrates, such as earthworms. Encysted larvae may persist in the invertebrates for months or even years. Birds eating the infected invertebrates then become infected themselves.

The infection is a major problem when turkeys and pheasants are reared on earth-floored pens. It is also a recognized problem in zoological collection.[3] Wilkinson,[4] reviewing the year 1986 at Chester Zoo, states: 'A current problem with breeding Starlings and Corvids in captivity is the susceptibility, particularly of young birds, to Gapeworm . . . Despite regular disinfection of the aviaries and worming of the adult birds, we have only partially controlled the problem. Young birds whilst still in the nest have been treated by presenting the worming agent (we use Panacur) injected into mealworms. The parents carry them to the young birds but this method cannot guarantee that all the young receive the correct dose. Where possible it is preferable to treat the nestlings direct, removing them from the nest for oral administration of the drug.'

We have seen similar problems in several collections, in Cornwall in particular, affecting Superb Starling *Spreo superbus* nestlings and Choughs. In an early case, a Chough was treated by rotating a turpentine-soaked feather in the trachea. This old method of treating poultry and gamebirds is inherently dangerous and seldom employed today, having been superseded by modern anthelminthics. It is noteworthy that the bird referred to here was treated by this method on two occasions and each time made a spectacular recovery, although this is not always the case. Furthermore, a year-old captive Chough which showed signs of respiratory distress, and was diagnosed as suffering from Gapeworm, was then treated with mebendazole ('Mebenvet') in its diet for 14 days. It failed to respond and died six weeks later. Post-mortem examination showed that it had a heavy infestation of *S. trachea*.

A variety of drugs is available for treating Gapeworm but, as above, the clinical response is not always good, especially where the drug is incorporated into food and water. Direct oral dosing as used by Bignal *et al.*[1] is preferable. However, a further problem which may occur is that treatment may cause large numbers of worms to become detached from the lining of the trachea and these may fall together and so form a plug. If this happens the bird is likely to die of asphyxia (V.R. Simpson., pers. obs.).

Choughs have been absent from Cornwall since 1973, and one of us (R.M.M.) is engaged in a study on the possible reasons for this. However, in 1986 a pair appeared just west of Plymouth on the Rame Peninsula. On 2 December, one of the birds, judged to be female, was seen to be wheezing slightly. Because of our experiences with captive birds, *Syngamus* infection was suspected. Faecal samples were collected from the birds' roost and feeding sites and examined microscopically. Bipolar eggs typical of *S. trachea* were present, reaffirming the impression that *Syngamus* was responsible for the respiratory distress. The bird's condition thereafter deteriorated steadily, and seemed to be exacerbated by wet weather. It appeared to be becoming critical and unlikely to recover naturally. The birds were feeding mostly on earthworms and beetles in a field of stubble-turnips which had been grazed by cattle (Meyer, in prep.). This was the single most favoured site, and we considered providing medicated food, but as mentioned earlier, this is not the preferred method. Also, had we done so the food would probably have been eaten by Magpies *Pica pica* and Starlings *Sturnus vulgaris* in the area.

In consultation with the Nature Conservancy Council, we proposed trapping the bird in order to dose it by mouth. Unfortunately it disappeared before this could be arranged. It was last seen on the morning of 4 January 1987, and we suspect it fell prey to a Peregrine *Falco peregrinus* during wet weather in the afternoon. Peregrines had been seen to make two earlier unsuccessful stoops on the Choughs, on 27 November and 2 December (the day symptoms were first noticed), and in poor weather, as noted, the ailing Chough's vigilance was seriously impaired. The remaining bird stayed in the area for a few weeks only and continued to thrive, including, incidentally, throughout a period of severe sub-zero temperatures.

Bignal *et al.*[1] surmized that the population of Choughs on Islay may be vulnerable to the effects of a chronic Gapeworm infection. They suggested that the high levels of infection in nestlings may be caused by parent birds either collecting food in an infected area, or concentrating on a particular item of food, such as earthworms, which may be heavily infected. We concur with this view but add that parasitic infections only normally become significant where the host is under stress, possibly from intercurrent disease or malnutrition, or where the parasitic challenge is very high, such as in captivity. Bignal *et al.* are, in effect, suggesting the latter. This is possible if species like Starlings and Magpies are contaminating the Chough's environment while themselves being less susceptible to the effects of infection. Brown & Thompson,[5] working on Golden Plovers *Pluvialis apricaria* and Lapwings *Vanellus vanellus*, suggest that dominant birds can identify infected prey; however, breeding birds might collect infected prey when under stress if, for example, feeding young becomes difficult, and first-time breeders may be more susceptible than experienced birds (E. Bignal, pers. comm.). It is therefore possible that pioneering birds, such as the recent Cornish Choughs, are more at risk than resident birds due to the stress of feeding in an unknown area. In Cornwall, *S. trachea* is certainly very common and has been seen in a number of post-mortem examinations in young wild Magpies and Carrion Crows *Corvus corone* (V.R. Simpson., unpubl. data). Despite being infected with Gapeworm, these species thrive.

Another possibility is that Choughs are suffering from Gapeworm because their immune reponses are impaired. This will occur due to stress, itself commonly seen as a result of malnutrition. The use of sub-optimal food resources by Choughs as a result of declining or degraded habitat could be a contributing effect.

ACKNOWLEDGMENTS

R.M.M. wishes to thank the Cornwall Bird Watching and Preservation Society for financial support during this study. Thanks also to Steve Madge and Drs Eric Bignal and Pat Monaghan of the Scottish Chough Study Group for their expert assistance, and Mij Meyer for typing the successive manuscript drafts.

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(MS received 5 February 1988; revised MS received 16 March 1988)

Note One Chough found dead at Marloes beach (Study Area W4) on 25th February 1991 was found to have 3 ? *Syngamus* nematodes, one with ? attached. Cause of death was not attributed directly to this infection

APPENDIX VIII

ECOLOGY OF THE CHOUGH *Pyrrhocorax pyrrhocorax* IN WEST WALES

REPORT TO THE NATURE CONSERVANCY COUNCIL
(Dyfed - Powys Region)

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March 1989

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GLASGOW G12 8QQ

INTRODUCTION

This report concerns mainly the 1988 breeding season of the Chough in West Wales but also gives indications (prior to fully worked up and analysed data) of their biogeography over an entire year. It builds on work begun in autumn 1987 (cf. Meyer, 1988 - where can also be found background information). The field work will continue to include the 1989 breeding season, and further documents will be produced for the nominated officer, S.B. Evans, following supplementary work to be done later this year at Glasgow University (see Future Plans).

The current inquiry complements my Ph.D. project which is looking specifically at the feasibility of re-establishing the Chough in Cornwall. I am suggesting that a viable Cornish population will help to conserve the Chough in the remainder of its N.W. European range by rejoining the relict French sub-population with the Welsh population. Currently, Pembrokeshire is the southern limit of the British population, but its tenure is precarious.

Prescribed Objectives

1. *To identify the main prey and foraging requirements of the Chough in the study areas listed under Methods.*
2. *To relate these findings with other areas of distribution in Wales and, by extrapolation, elsewhere and to consider habitat management.*
3. *To investigate range and prey exploitation during the breeding season at the above sites.*

In short, the main requirements were to obtain precise details of the chough's feeding and breeding ecology and establish a replicable methodology.

METHODS

The study areas in Pembs. (Fig. 1) are:

A. MWNT - CEMAES
B. STRUMBLE HEAD - PENBWCHDY
C. SOLVA - NEWGALE (St Davids)
D. MARLOES PENINSULA

The study areas were selected to include key Chough sites and for their relevance to my Cornish research. They were chosen to represent a good range of mainland Pembrokeshire biotopes but excluded the Castle Martin - Stackpole NNR and offshore islands on account of existing studies (Gamble & Haycock, 1988) and their non-relevance to Cornwall. Within each study area, resource use, range exploitation, food selection, and the relevant background invertebrate faunas were investigated.

Simplified Methodolgy

1. *Direct observational data derived from 'pursuit' periods (see below) and nest-watching; enabling habitat preferences, feeding efficiency within and between different habitats, and social behaviour at different seasons to be assessed.*
2. *Collect and analyse chough faeces/pellets.*
3. *Invertebrate sampling by soil sampling and hand searching, to indicate the available prey spectrum and relative abundancies.*

4. *Study areas were visited every six weeks. Visits were not terminated until sufficient data were obtained - usually in two or three days.*

Bird were sought and their ranges established within study areas by walking a fixed route which explored as fully as possible all cliff lands. Outside the breeding season and in hilly terrain the birds were often difficult to find. The Chough exists in low numbers and is a highly mobile species with quite extensive ranges, typically 3-5 kilometres of often indented coastline. Monitoring their movements for a full day was seldom possible, and I developed a system of 'Dedicated Search Time' (DST) which involved walking a linear transect-like route based upon the coastal path; in the event of no Choughs being found successive swathes inland were searched until it was assumed that the birds had been missed, and the process was repeated. With increased experience, it was possible to search in order of decreasing success probability. Range and resource exploitation were noted using habitat sub-categories developed specifically for Choughs from broader conventional classifications (such as NVC). These data are quantified, map-marked and summarised in this report.

Study ranges were determined by the birds' movements and, beyond that, by visible limits. As may be seen from the range exploitation maps, very few observed flight paths led beyond confirming that the ranges were satisfactorily covered.

Explanations of terms used in habitat selection figures

C	CLIFFS (inclusive of all 'C' sub-categories)
Cu	CLIFFS - unspecified
Cs	CLIFFSLOPE (any gradient between the near vertical and near horizontal) - usually vegetated by maritime grass
Ct	CLIFFTOP - the near horizontal lip of the cliff: short compact vegetation often showing the effects of trampling (eg. paths) and exposure
Ce	CLIFFEDGE - ecotone at the vertical lip of the clifftop: heavily eroded, unvegetated and unstable
Cc	CLIFF CREVICE - strata or pockets/zones of earth surrounded by rock (ie. maximised area of rock/earth interface)
Cb	CLIFF-SEABIRD community - Atriplex/Beta/Lavatera/Rumex etc
P	PASTURE - all permanent or old term leys ()10 years)
A	ARABLE - mainly cereal stubble
H	HEATH - maritime, open
AN	ANTS - a difficult sub-category because of ant presence across the range - here refers to a habitat heavily influenced in its physiography by ant activity - and is not to be read as a measure of the importance of ants, which certainly exceeds it.
Pt	PATHS - heavily trampled and eroded ground with much exposed substrate.*

Fresh faeces were collected whenever possible after the birds departure. Later feeding sites were revisited and investigated for prey selection and invertebrate faunas. No accessible roost sites were found; nest sites were generally used as main roosts.

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* *'Path effect' occurs across much of the habitat range, and a more detailed analysis of this and other effects (eg. exposed earth) should reveal their importance.*

Fig. 1.

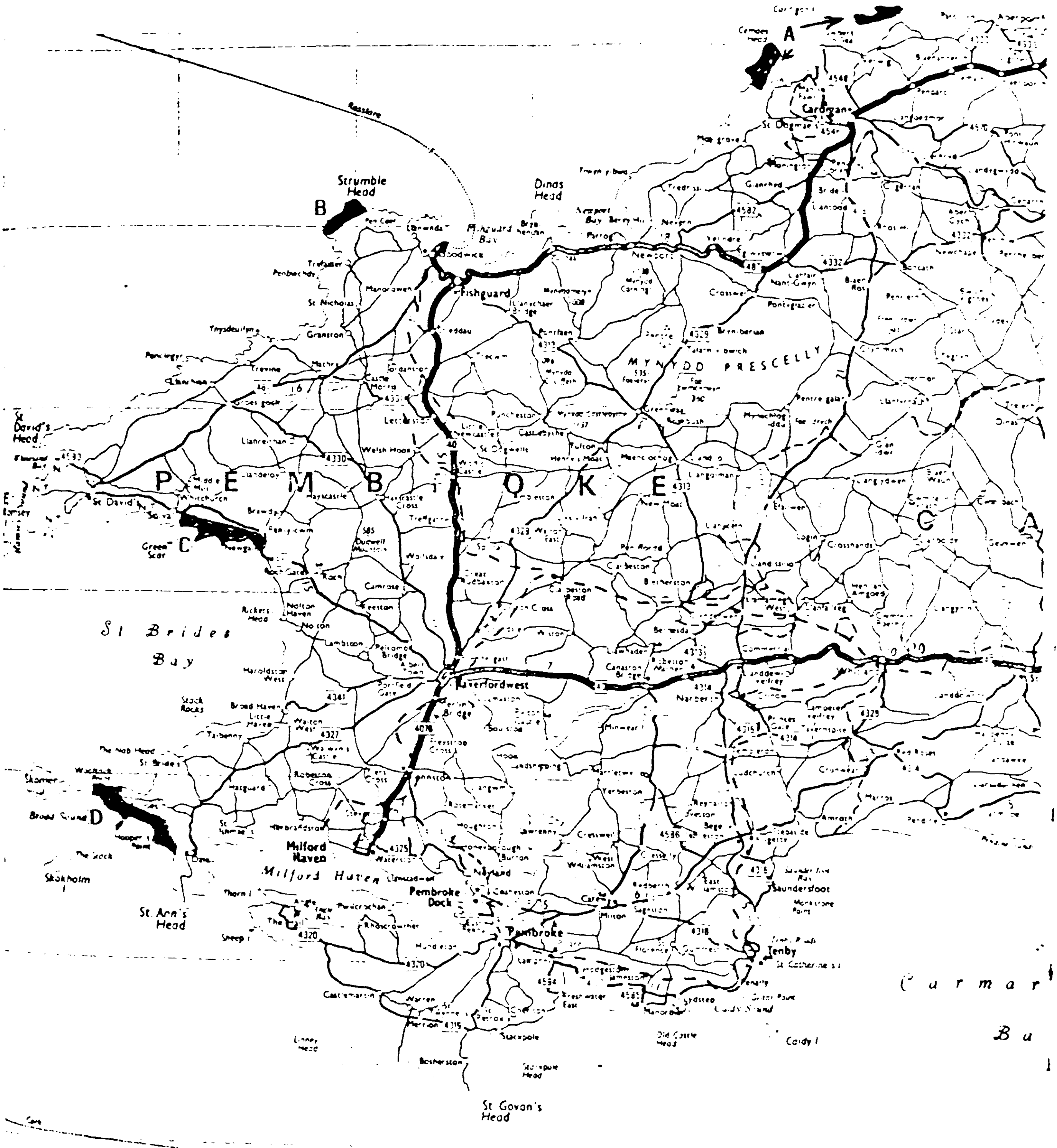
West Wales and location of four study areas.

A. Mwnt and Cemaes

B. Strumble Head - Penbwchdy

C. Solva - Newgale (St. Davids)

D. Marloes Peninsula


A
Cemaes Head
Cardigan
St Dogmaels
B
Strumble Head
Dinas Head
Fishguard Bay
Goodwick
Fishguard
Newport
Penbwchdy
St Nicholas
Mathry
Trevine
MYNYDD PRESCELLY
St David's Head
Ramsey
St David's
Solva
C
Green Scar
Newgale
P E M B R O K E
Roch
St Brides Bay
Haverfordwest
Narberth
Whitland
Broad Haven
Little Haven
The Nab Head
St Brides
Skomer
D
Broad Sound
Skokholm
St Ann's Head
Dale
Milford Haven
Neyland
Pembroke Dock
Pembroke
Castlemartin
Stackpole
Bosherston
St Govan's Head
Saundersfoot
Tenby
Caldy I
Carmar
Bay

Faeces were teased apart in water and with the aid of a X6.5-15.0 binocular microscope remains were identified to family or genus level, many were saved for onward identification to a higher level, and this work is in hand. The higher magnification (with transmitted light) was used for finding earthworm chaetae.

Prey and potential prey were sampled following Bullock's methodology (1980): ie. prey checks and soil-sampling at specific feeding sites. Together this reveals preferred prey and habitats, and relative abundancies and seasonal variations within them. Soil sampling is time-consuming and tedious but it does mimic the Chough's feeding behaviour, and is biased positively in selection enabling instant sampling at recently vacated feeding sites (which are compared with apparently similar but unused sites nearby). Additionally, it does not require destructive equipment (pitfall traps) to be set up and left in situ for long periods. Analysis of this work is in hand.

As the study progressed and birds were found more easily, less time was spent in negative DST, and 'Chough Minutes' (CM's: no. minutes X no. of Choughs observed) were refined to 'Feeding Chough Minutes' (FCM's: no. minutes X no. Choughs feeding) to convey a more meaningful relationship between Choughs and their habitats. This assumes that the criteria Choughs use to select resting and preening sites are less important than those employed in the selection of feeding sites. Often, of course, they are the same.

Individual birds or flocks were studied non-intrusively using a X20-60 Opticron telescope and wide-angle scanning binoculars. Birds were occasionally sometimes unwittingly disturbed when approached blind or if I happened to be standing in or near a desired Chough location. All such disturbances plus the many more caused by casual visitors and walkers together with inter- (and occasionally intra-) specific interactions were noted with their respective outcomes.

The Chough year is divided into three biological seasons: winter (November - February), breeding (March - June), and post-breeding (July - October) as in Bullock, 1980.

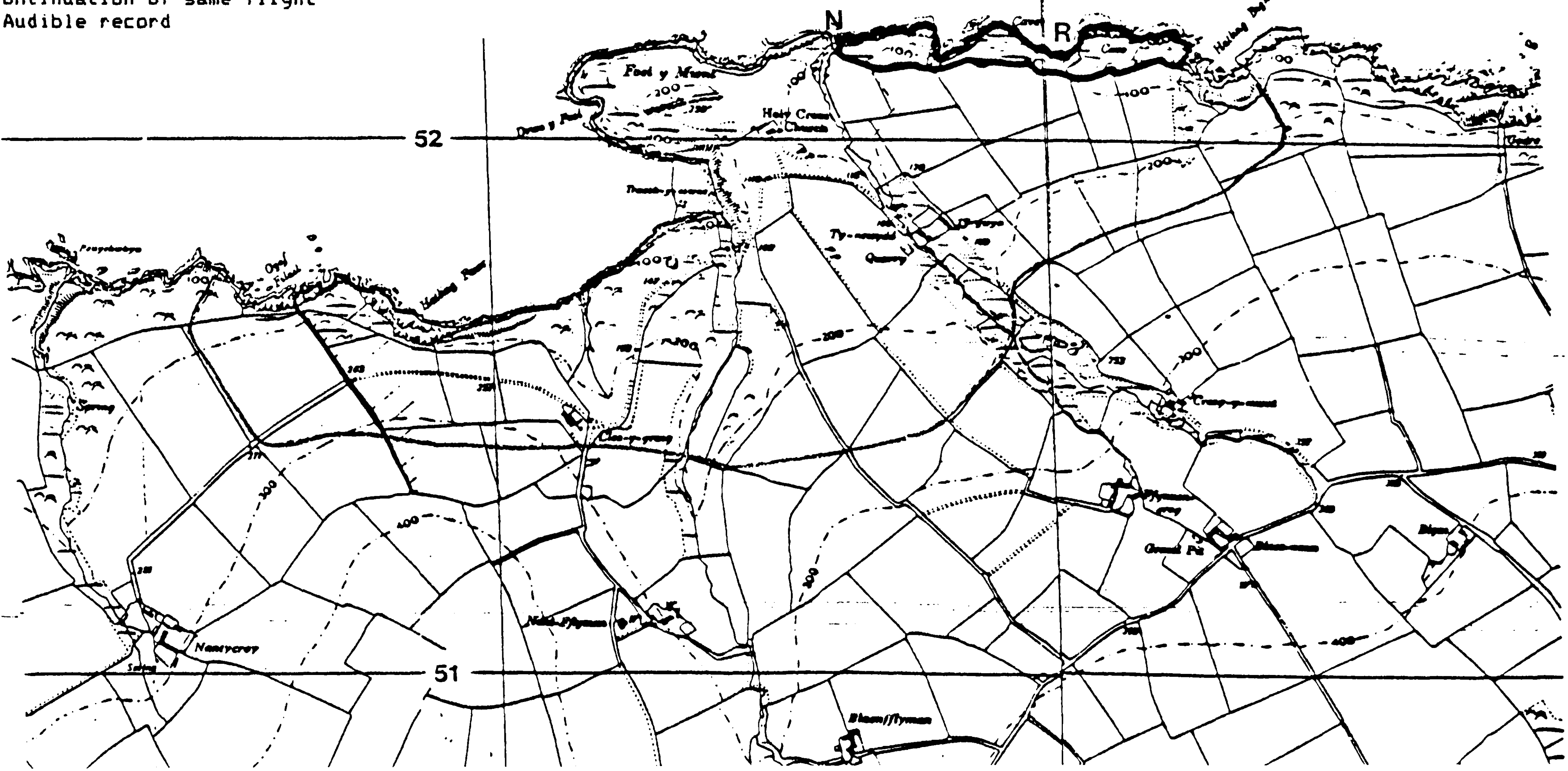
RESULTS

Study Area A: Mwnt - Cemaes

This site (Fig. 2) at the north of the region spans the Pembrokeshire - Ceredigion boundary and the Teifi estuary but had to be treated as two separate sites due to travel distances. Cemaes is a classic cape-like headland which is now the focus of a conservation initiative. The area comprises outcropping rock, a small island (Cardigan I.) and an agricultural complex of rough pasture, arable and improved pasture fringed by historically grazed coastal slopes and cliffs of known importance to Choughs. Pursuit-effort was concentrated at Cemaes due to bird-location problems at Mwnt outside the breeding season.

Fig. 2.
Study range and exploitation in Study Area A.
2a. Mwnt - Breeding season; 2b. Cemaes - winter;
2c. Cemaes - breeding season; 2d. Cemaes - Post-breeding season.

Large dot - observed important feeding site (>10 events)
Small dot - possibly secondary feeding site (<10 events)
N(n) - Nest site
R - Roost or shelter site
V - Visible record unconnected with observed feeding event
>> shows direction of one flight
 > continuation of same flight
A - Audible record



N
R
Foel y Mwnt
Holy Cross Church
52
Quarry
Ground Pit
Nantycroy
51
100
200
300
400

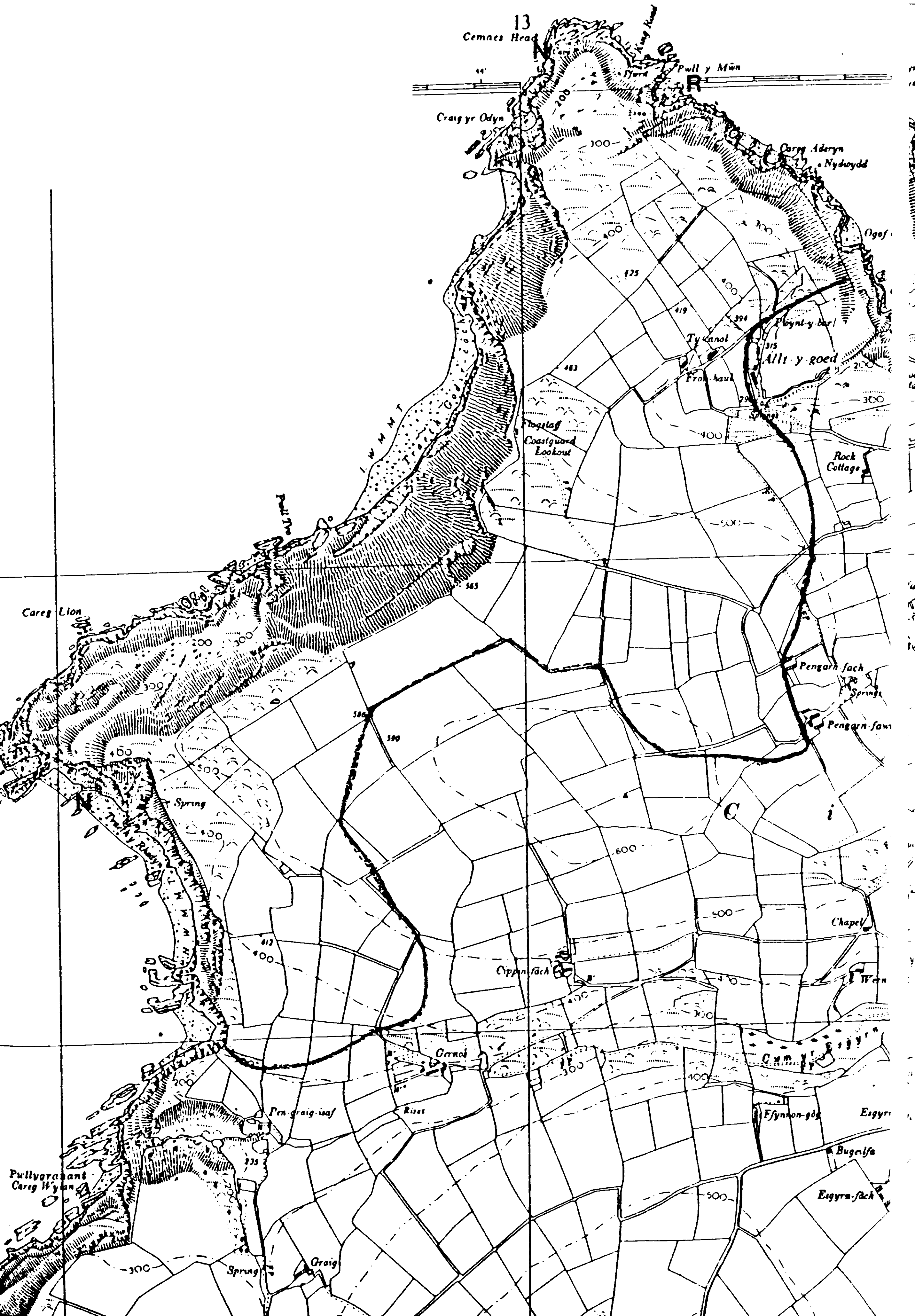

13
Cemaes Head
Pwll y Mŵn
R
Craig yr Odyn
200
300
Carreg Aderyn
Nydwydd
Ogof
400
425
419
394
Ty-canol
Allt-y-goed
Fron-haul
315
483
Flagstaff
Coastguard Lookout
Springs
Rock Cottage
500
565
Pwll Trw
L W M M T
Careg Lion
Pengarn-fach
Springs
Pengarn-fawr
C
i
580
590
Spring
600
612
Cippyn-fach
Chapel
Wern
Cwm yr Esgyrn
Ernol
Pen-graig-isaf
Rises
Ffynnon-gôg
Esgyrn
Bugeilfa
Esgyrn-fach
235
Pullygranant
Careg Wylan
Spring
Graig
N

Fig. 2a. Mwnt - breeding season

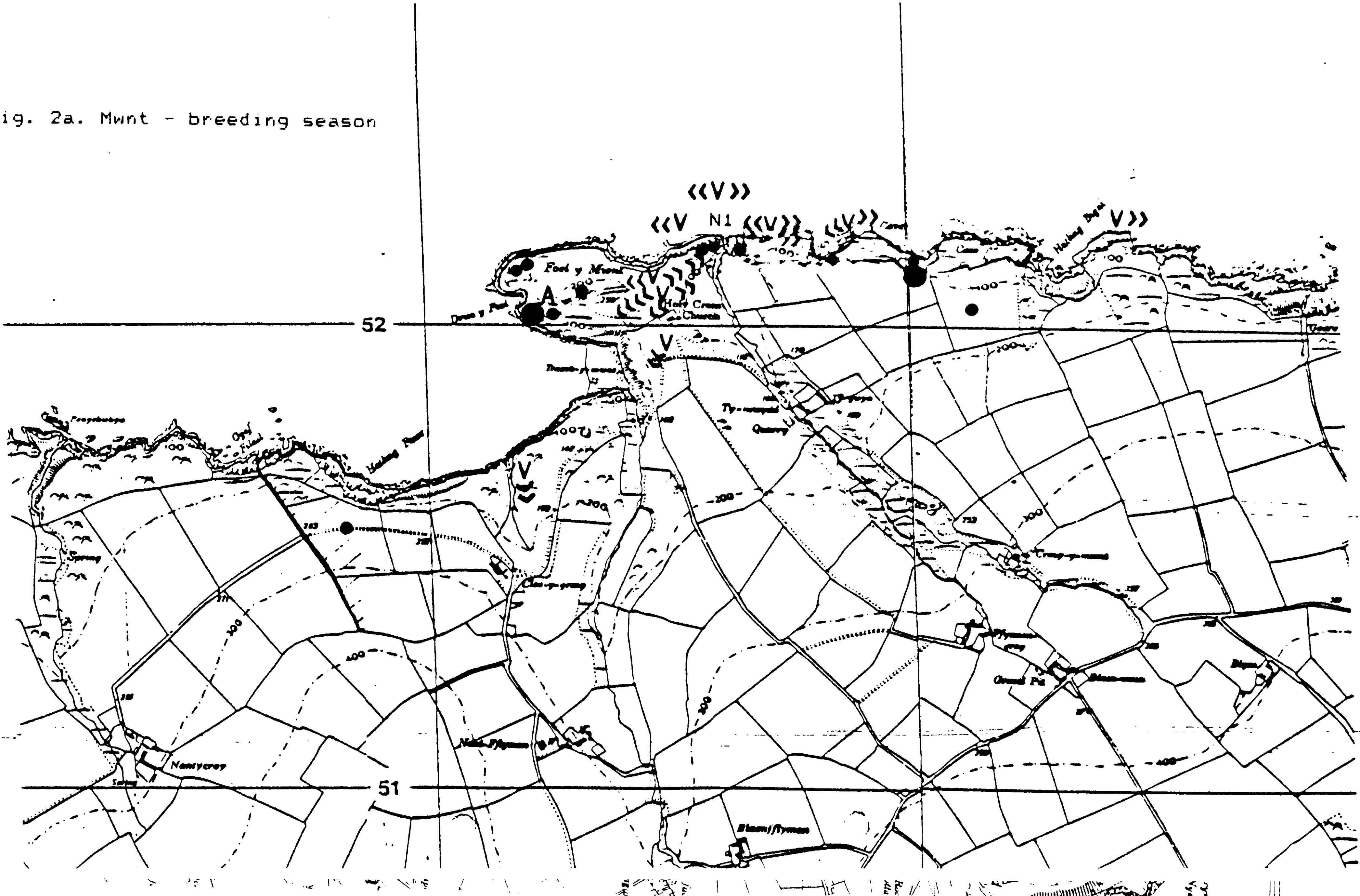

((V))
((V
N1
((V))
((V))
V))
A
V
V
Foel y Mwnt
Holy Cross Church
52
51
100
200
300
400
Nantycroy

Fig. 2a. Winter

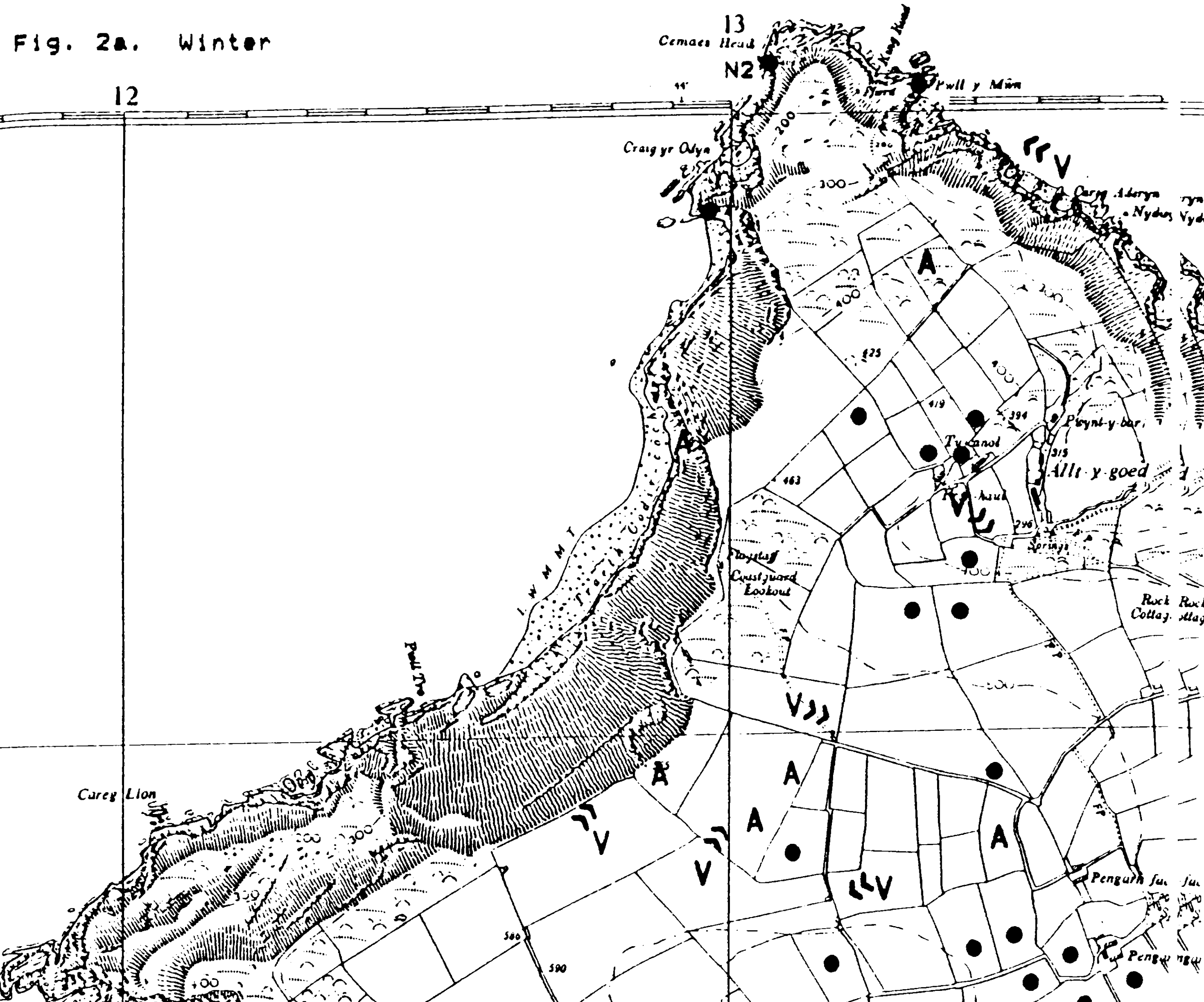
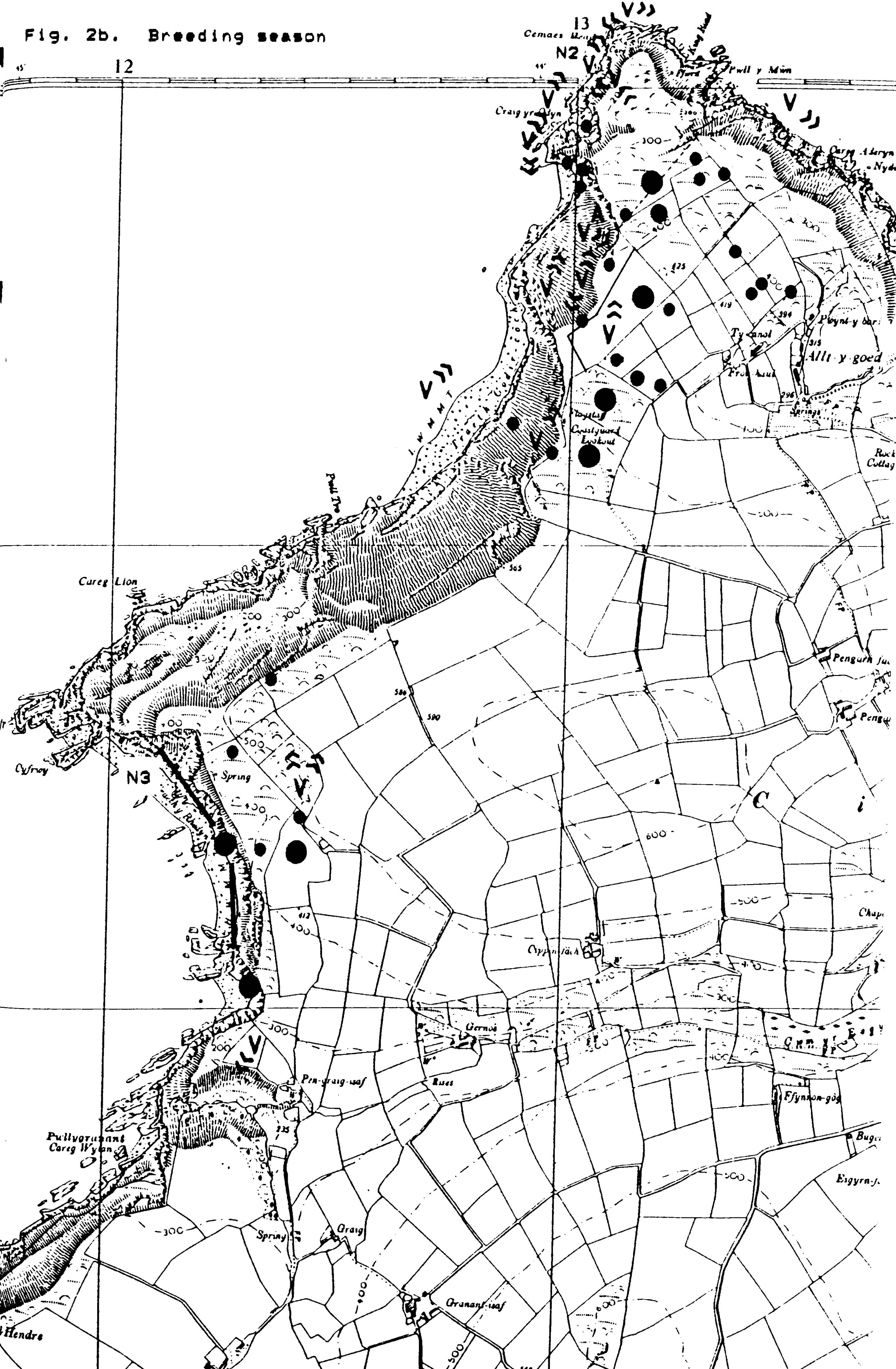

13
12
Cemaes Head
N2
Pwll y Mŵn
Craig yr Odyn
Careg Aderyn
Tycanol
Allt-y-goed
Springs
Flagstaff
Coastguard Lookout
Rock Cottage
Pwll Tŷ
Careg Lion
Pengurn
N3
Spring
Cyfrwy
Gernos
Pen-graig-isaf
Rises
Ffynnon-gôg
Chapel
300
400
500
600
A
V
C

Fig. 2b. Breeding season



12
13
Cemaes Head
N2
Pwll y Mŵn
Craig yr Adyn
Careg Aderyn
Ty canol
Allt y goed
Coastguard Lookout
Pwll Tro
Careg Lion
Cyfrwy
N3
Spring
600
500
400
300
Gernos
Pen-graig-isaf
Ffynnon-gôg
Pullygranant
Careg Wylan
Graig
Granant-isaf
Hendre

Fig. 2c. Post-breeding season

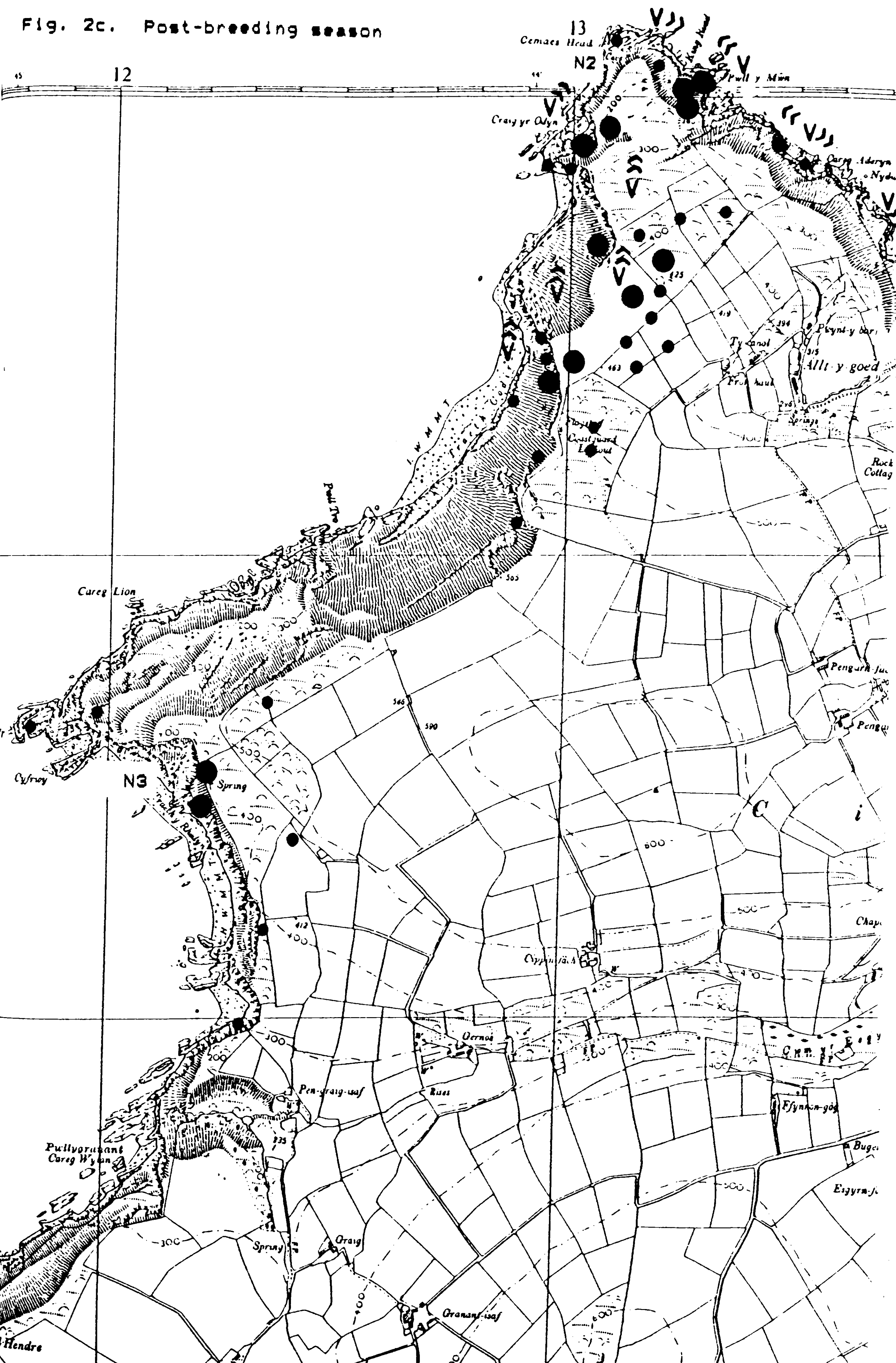

13
Cemaes Head
N2
Pwll y Mŵn
12
Craig yr Odyn
Carreg Aderyn
Nydu
200
300
400
425
419
463
394
315
Ty-canol
Pwynt-y bar
Allt-y-goed
Fron hual
Springs
Pwll Tro
Coastguard Lookout
Rock Cottag
505
Careg Lion
Pengurn
Cyfrwy
N3
Spring
546
590
600
C
i
412
Cippyn fach
Chap
Cwm-yr-Eglwys
Oernos
Rises
Pen-graig-isaf
Ffynnon-gôg
Bugel
Esgyrn-fa
Pullyoruant
Careg Wylan
335
Spring
Graig
Granant-isaf
Hendre

Table 1. The Chough's diet in Study Area A as shown by faecal analysis (a), with details of the beetle component (b). Figures in (a) are percentages of occurrences per faecal sample. Figures in (b) are percentages of beetle positive samples.

Food	Winter	Breeding	Post-breeding	Year mean
(a)				
Beetles (all ages)	100	85	83	89
Fly larvae	23	15	17	17
Earthworms	10	6	33	12
Other + Ants	0	11	33	12
Cereal grains	29	0	6	10
(b)				
Beetle adults	87	63	100	69
Beetle larvae	32	50	0	32
Scarab's all ages	35	43	80	42
No. faecal samples	31	54	18	103

NB. Incomplete results

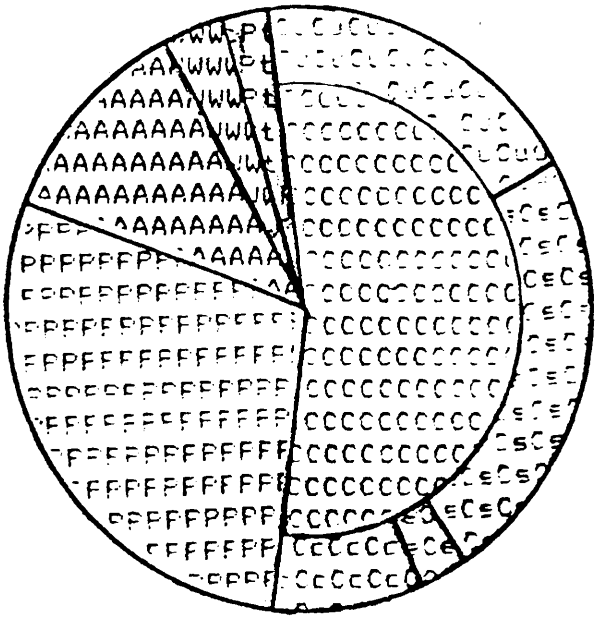


Fig. 3. Proportional selection of habitats by Choughs over one year in Study Area A (excluding Mwnt) with no. of FCM's. *See Methods for classification notes.*

Key		FCM's
Cu	Cliffs unspecified	935
Cs	Cliff-slope	1162
Ce	Cliff-edge	140
Cc	Cliff-crevice	401
C	Cliffs (all)	2636
P	Pasture	1426
A	Arable	578
W	Wall-bank	166
Pt	Paths	122
	Total	4930

There were three nest sites within the area, two (N1 and N3) were unsuccessful possibly due to disturbance by close human passage (N1) and by Peregrines Falco peregrinus nesting nearby (N3). Site N2 was not seen to be disturbed, and produced four young.

The increased dependence on inland fields during the winter months is evident. This moderates in early spring when adults move to breeding stations and utilise cliffs, coastal slopes and pastures. Habitat selection over a year is shown in Fig. 3. During the winter, cereal grain and earthworms complement the usual insectivorous food. Beetles are of vital importance at all times - appearing in about 90% of all faeces collected (Table 1). Earthworms increase in importance in the post-breeding season: rising to 33% occurrence. Ants are perhaps the key component during the breeding and post-breeding season; a fact not as yet reflected in tabulated results (see Future Plans).

The preference of Choughs to feed on paths or otherwise trampled and eroded ground and/or short and compacted vegetation was very noticeable at this site. Selection of such areas within the pasture fields suggests the need for a heavier grazing regime.

Study Area B: Strumble Head - Penbwchdy

Strumble Head is a popular seabird watching site, and as at Cemaes is dominated by a caped headland. It has a reputation for being especially rich in breeding Choughs - as many as 7 pairs, according to one local source. In 1988, however, only one pair nested (N4); producing 3 young. This pair ranged over almost the entire study area which comprises an extremely rich mosaic of natural and semi-natural habitats (Fig. 4). During the breeding season, the birds ranged over at least 4 km, utilising a variety of habitat types (Fig. 5).

Meaningful winter records are deficient due to a low search success rate and the mild winter of 1988/9. The physical similarities between Study Areas A and B would, however, suggest a similar pattern of habitat use. One significant difference between the two areas is the islet which is near N4 and abuts Pen Brush. It has a classic cliff-bird flora rarely found on the mainland, and was the main observed winter feeding haunt. Unfortunately it was not possible to sample directly this site, but analysis of faecal remains showed that the birds were feeding on earthworms and the typical invertebrates of such a botanical community: amphipods, woodlice, millipedes etc. (Table 2). Otherwise, as in Study Area A, beetles were the most important food category overall, earthworms being the only other food to figure prominently, possibly balancing the decreased emphasis on cereals (see Discussion and Table 5).

Study Area C: Solva - Newgale (St. Davids)

Situated along the coast south of St. Davids. Study Area C does not have one central head but two smaller points: Dinas Fawr and Dinas Fach, each of which, supported a nest site (N5 & N6) in 1988 (Fig. 6). Past records infer a higher density.

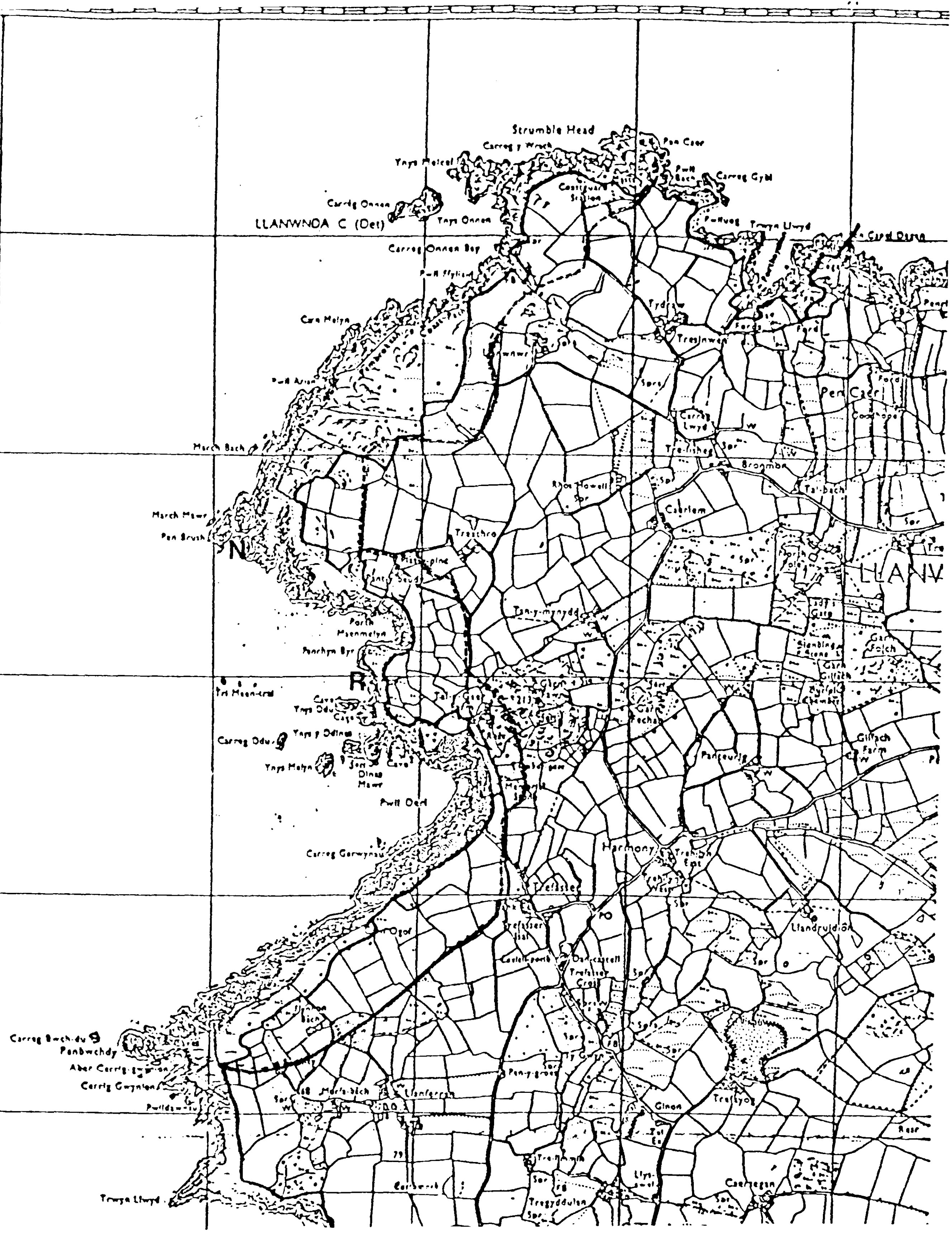
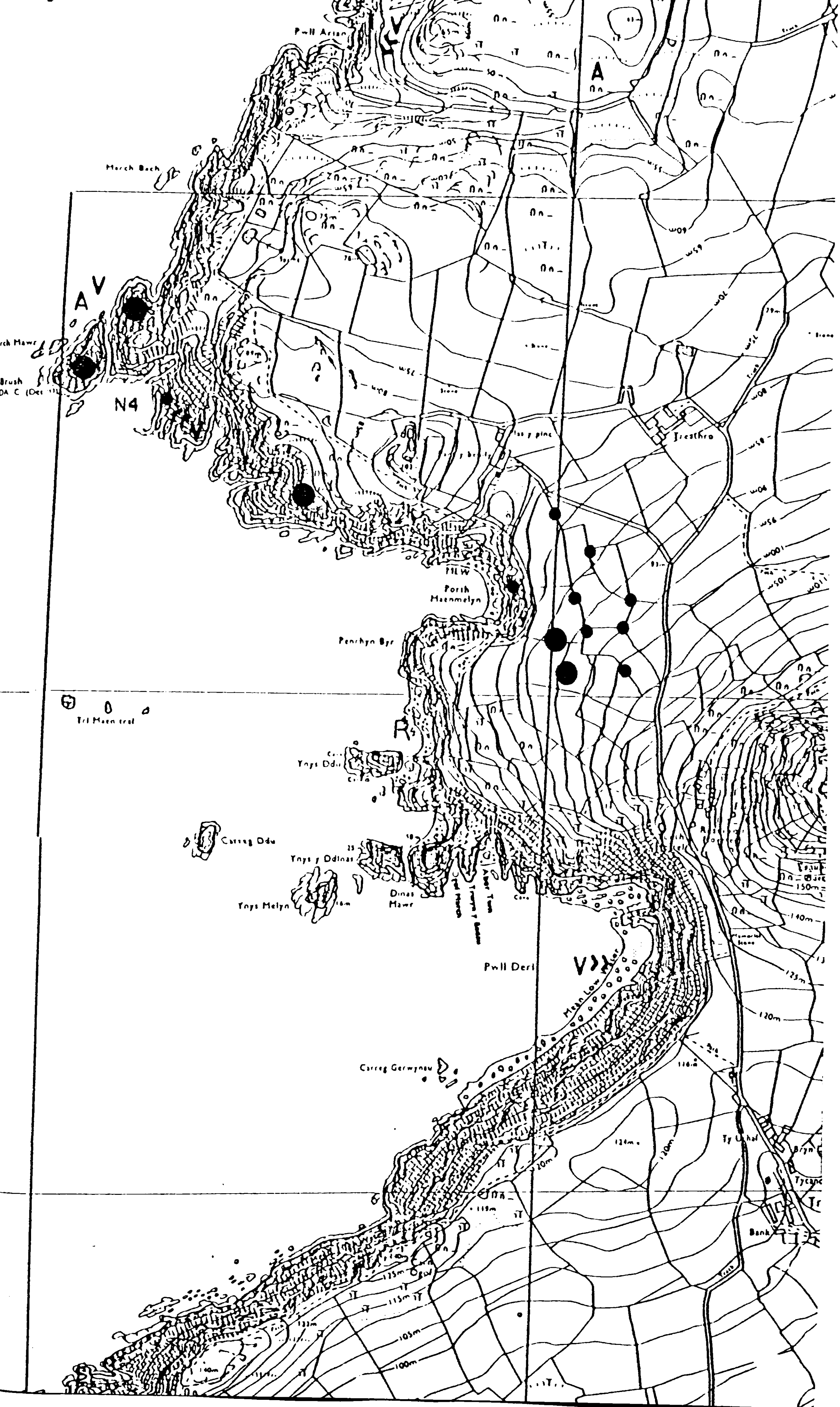

Strumble Head
Carreg y Wrach
Ynys Meicel
Pen Caer
Pwll Bach
Carreg Gybi
Carreg Onnen
LLANWNDA C (Det)
Ynys Onnen
Coastguard Station
Pwllwag
Trwyn Llwyd
Carreg Onnen Bay
Pwll Ffyliaid
Carn Melyn
Tresinwen
Pen Caer
Pwll Arian
March Bach
Rhos Howell
Carlem
Tal-bach
March Mawr
Pen Brush
N
Treathro
LLANW
Porth Maenmelyn
R
Tri Maen-trai
Ynys Ddu
Carreg Ddu
Ynys y Ddinas
Ynys Melyn
Dinas Mawr
Pwll Deri
Carreg Gorwynion
Harmony
Ogof
Llandruidion
Carreg Herbwchdy
Penbwchdy
Aber Cerrig-gwynion
Carreg Gwynion
Pwlldawnau
Morfa-bach
Llanferran
Ginon
Tresissyllt
Trwyn Llwyd
Tregyddulan
Caerhegyn

Fig. 4.
Study range and exploitation in Study Area B (Strumble).
4a. Winter; 4b. Breeding season; 4c. Post-breeding season

Large dot - observed important feeding site (>10 events)
Small dot - possibly secondary feeding site (<10 events)
N(n) - Nest site
R - Roost or shelter site
V - Visible record unconnected with observed feeding event
>> shows direction of one flight
> continuation of same flight
A - Audible record

Fig. 4a. Winter


Pwll Arian
A
V
March Bach
A
V
rch Mawr
Brush
N4
MLW
Porth Maenmelyn
Penrhyn Byr
Trefathro
Tri Maen-trai
R
Ynys Ddu
Carreg Ddu
Ynys y Ddinas
Ynys Melyn
Dinas Mawr
Pwll Deri
V
Carreg Gerwyneu
Ty Uchaf
Bank
150m
140m
125m
120m
115m
105m
100m

4b. Breeding season

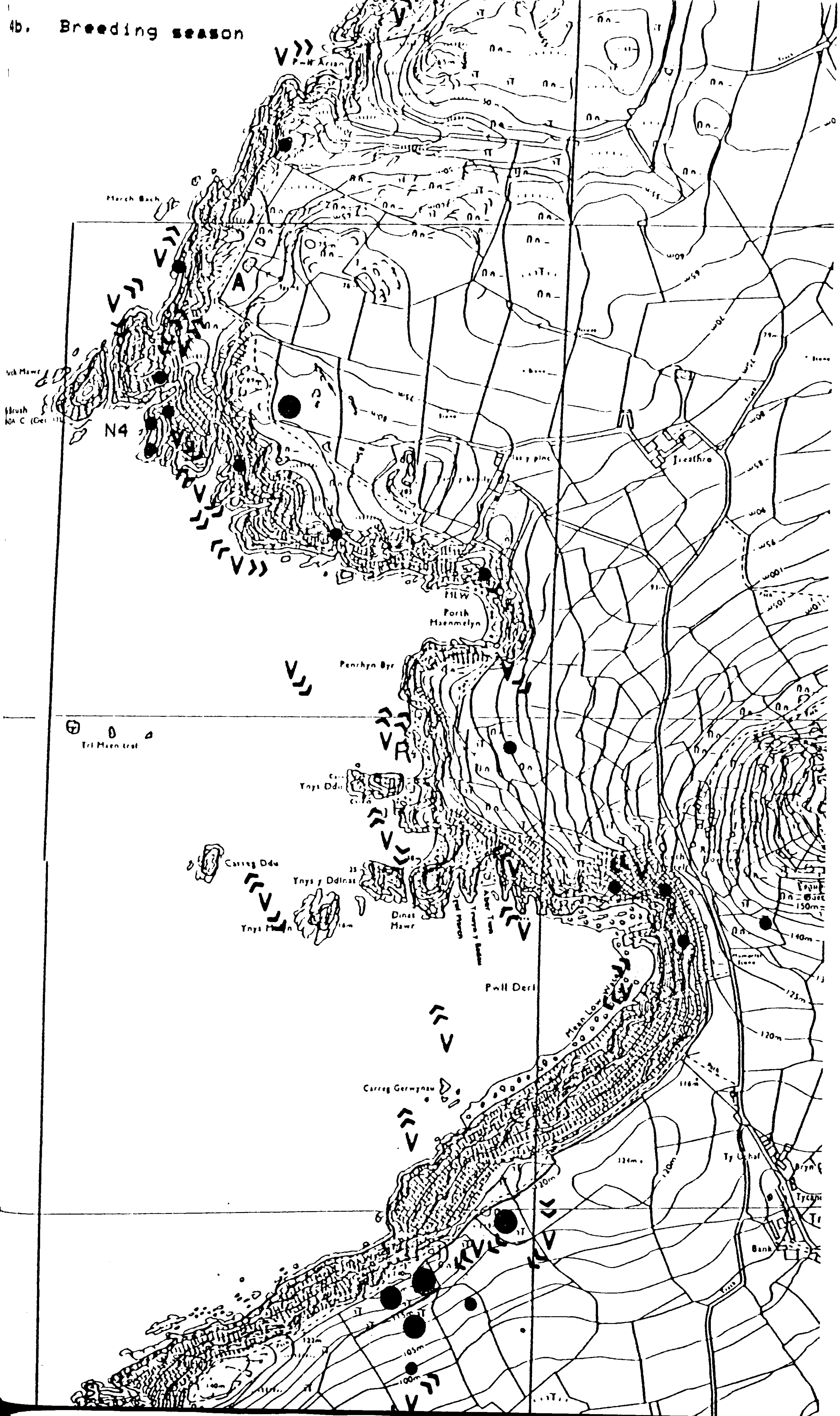

V
V
March Bach
A
N4
Porth
Maenmelyn
Penrhyn Bŷr
Tri Maen trai
V
R
Ynys Ddu
Carreg Ddu
Ynys y Ddinas
Ynys Meicel
Dinas
Mawr
Aber Twm
Pwll Deri
Carreg Gerwynau
Treathro
Ty Uchaf
Bank
150m
140m
125m
120m
110m
105m
100m

Fig. 4c. Post-breeding season

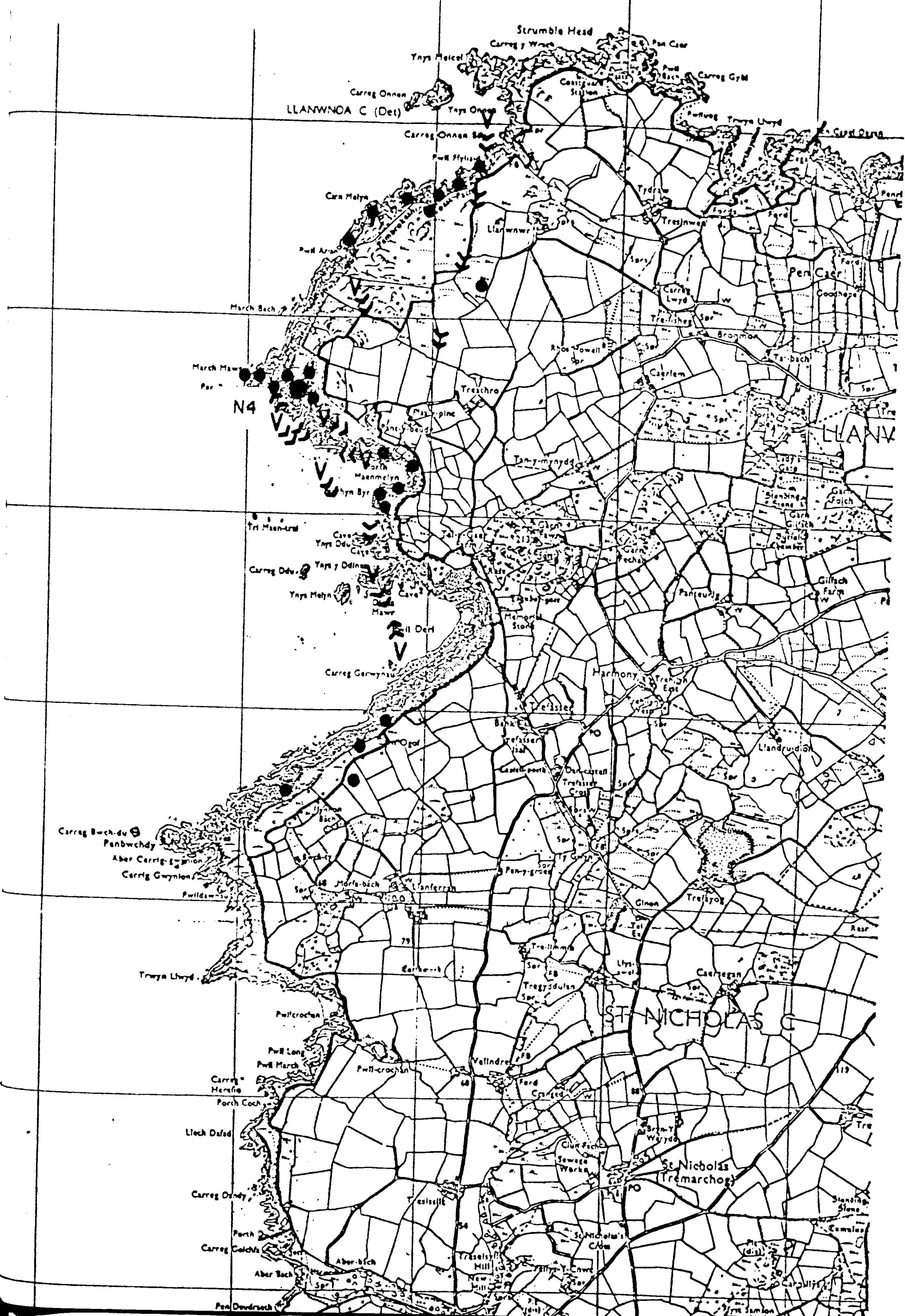

Strumble Head
Carreg y Wrach
Pen Caer
Ynys Meicel
Carreg Gybi
Carreg Onnen
LLANWNDA C (Det)
Ynys Onnen
Carreg Onnen Bay
Pwll Ffyliaid
Carn Melyn
Llanwnwr
Tydraw
Tresinwen
Pwll Arian
Pen Caer
Carreg Lwyd
March Bach
Trefisheg
Rhos Powell
Caerlem
March Mawr
N4
Trenewydd
Plas-y-pinc
Pant-y-beudy
Tal-y-mynydd
LLANW
Porth Maenmelyn
Penrhyn Bychan
Tri Maen-trai
Ynys Ddu
Ynys y Ddinas
Carreg Ddu
Ynys Melyn
Ogof Mawr
Pwll Deri
Carreg Gerwyn
Harmony
Trefasser
Carreg Bwch-du
Penbwchdy
Aber Cerrig-gwynion
Cerrig Gwynion
Pwlldawnau
Llanferran
Morfa-bach
Trwyn Llwyd
Pwllcrochan
Pwll Long
Pwll March
Carreg Herefio
Porth Coch
Llech Dafad
Carreg Ddu
Porth
Carreg Golchfa
Aber Bach
Pen Deudraeth
Velindre
Trelimmin
Tregyddulan
Caerhegan
ST NICHOLAS C
St Nicholas (Tremarchog)
Trefsyog
Llandruidion
Treseisyllt
Penysgwarne
Castell-coch
Trefasser Cross
Standing Stone

Table 2. Chough diet in Study Area B as shown by faecal analysis. Figures are percentages of occurrences per faecal sample.

Food	Winter	Breeding	Post-breeding	Year mean
Beetles (all ages)	94	69	100	84
Earthworm	56	8	50	35.5
Fly larvae	6	15	0	10
Cereal grains	6	0	0	3
Ants	6	0	0	3
Woodlice	6	0	0	3
Millipedes	0	8	0	3
Earwigs	0	8	0	3
Spiders	0	8	0	3
No. faecal samples	16	13	2	31

NB. Incomplete results

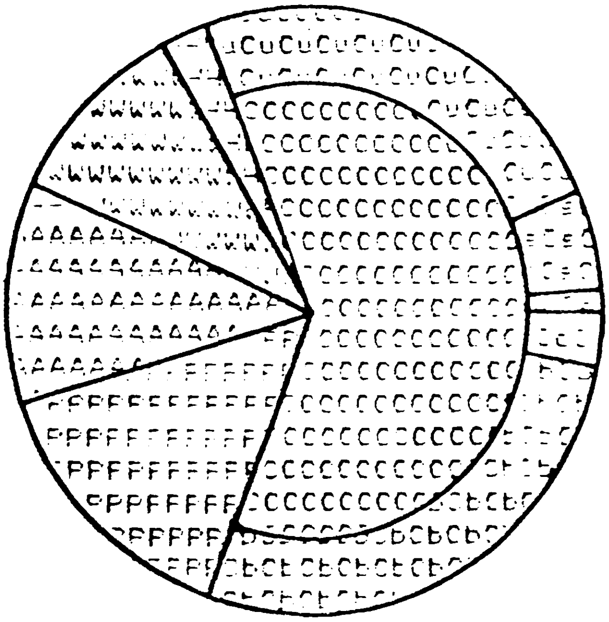


Fig. 5. Proportional selection of habitats by Choughs over one year in Study Area B with no. of FCM's *See Methods for classification notes.*

Key		FCM's
Cu	Cliffs unspecified	960
Cs	Cliff-slope	212
Ce	Cliff-edge	43
Cc	Cliff-crevice	114
Cb	Cliff-bird flora	1094
C	Cliffs (all)	2423
P	Pasture	573
A	Arable	462
W	Wall-bank	398
H	Heath	115
	Total	3971

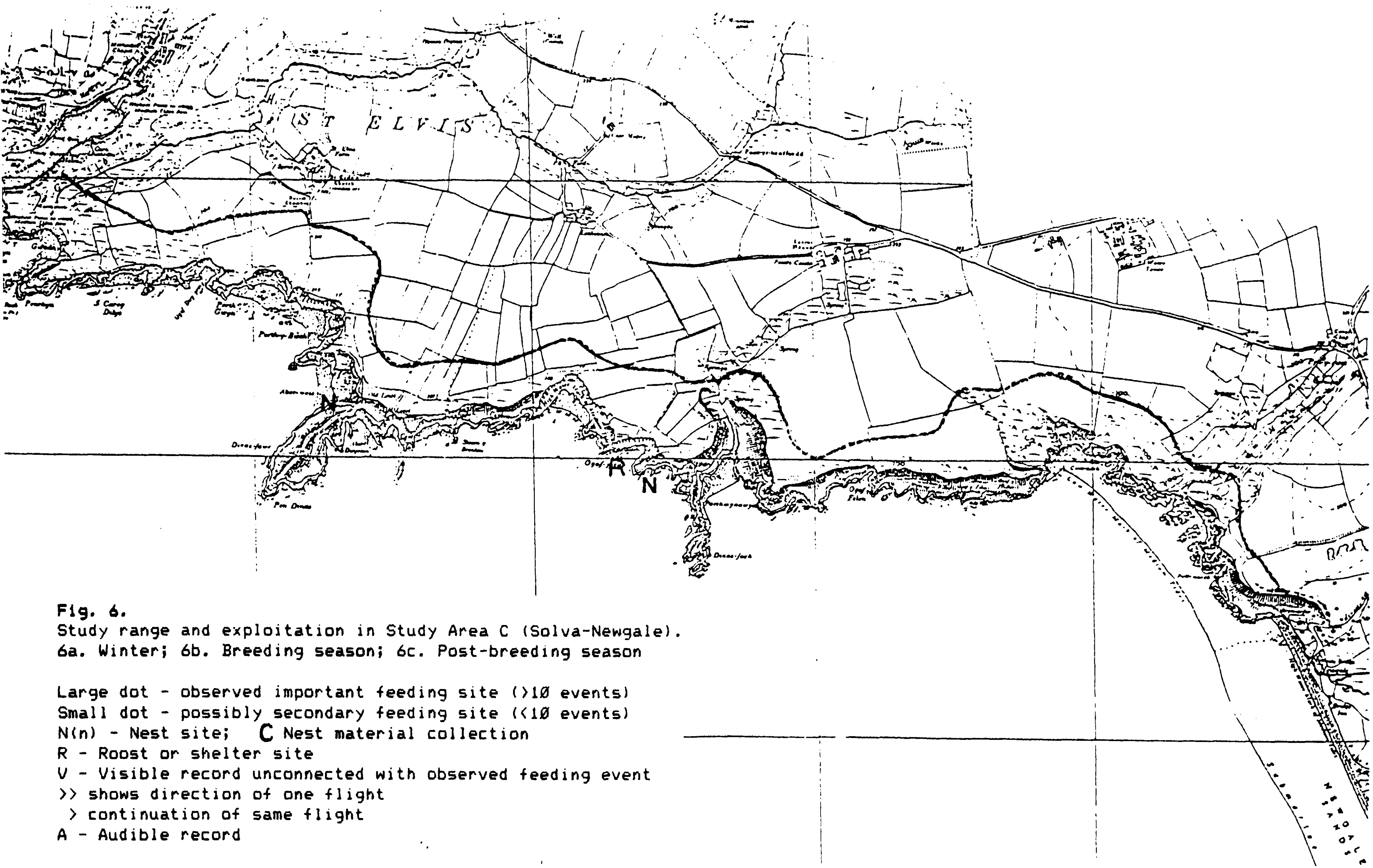
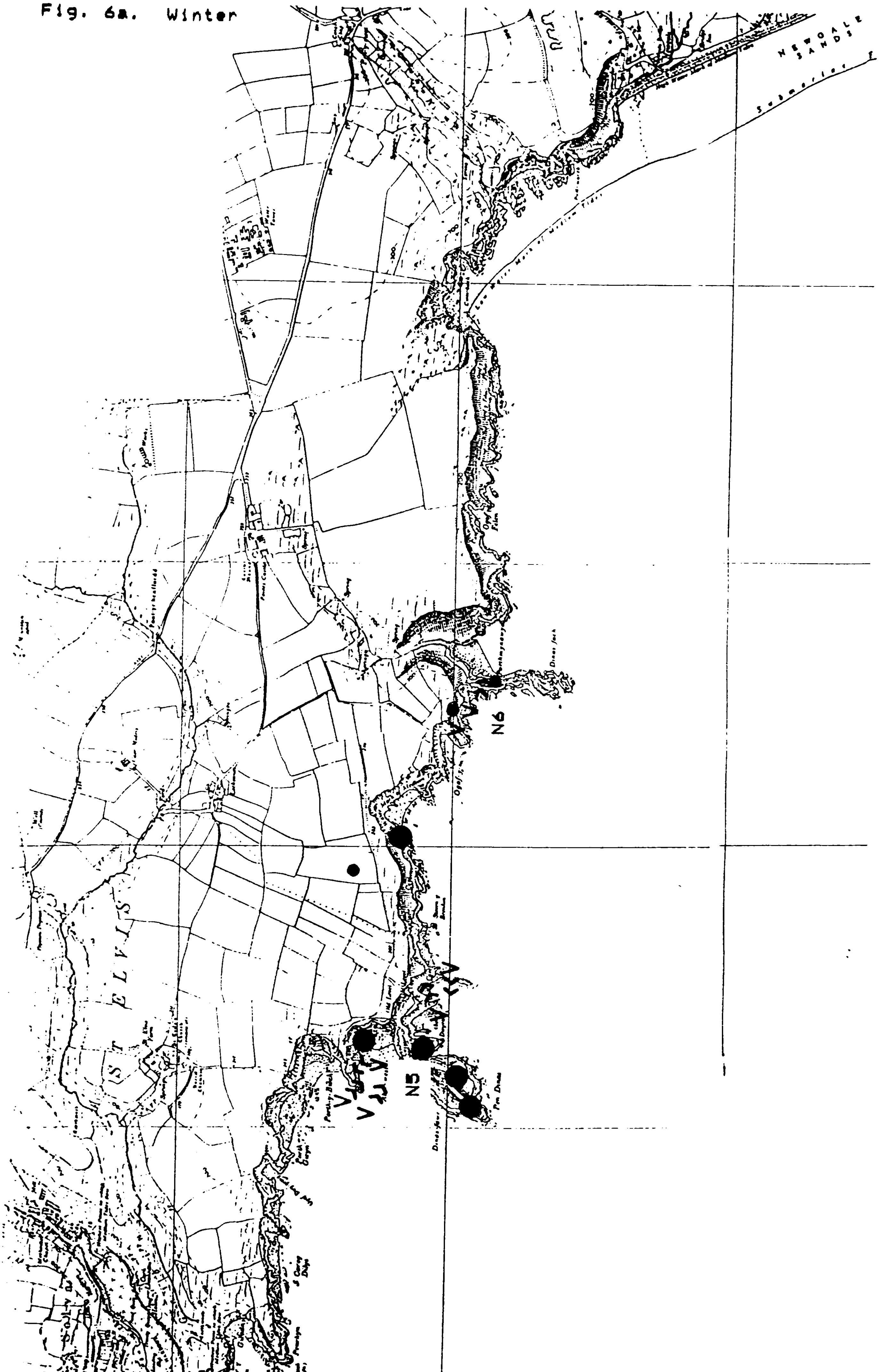


Fig. 6.
Study range and exploitation in Study Area C (Solva-Newgale).
6a. Winter; 6b. Breeding season; 6c. Post-breeding season

Large dot - observed important feeding site (>10 events)
Small dot - possibly secondary feeding site (<10 events)
N(n) - Nest site; **C** Nest material collection
R - Roost or shelter site
V - Visible record unconnected with observed feeding event
>> shows direction of one flight
 > continuation of same flight
A - Audible record

Fig. 6a. Winter


NEWGALE SANDS
N6
N5
ST ELVIS
Dinas Fach
Pen Dinas

6b. Breeding season

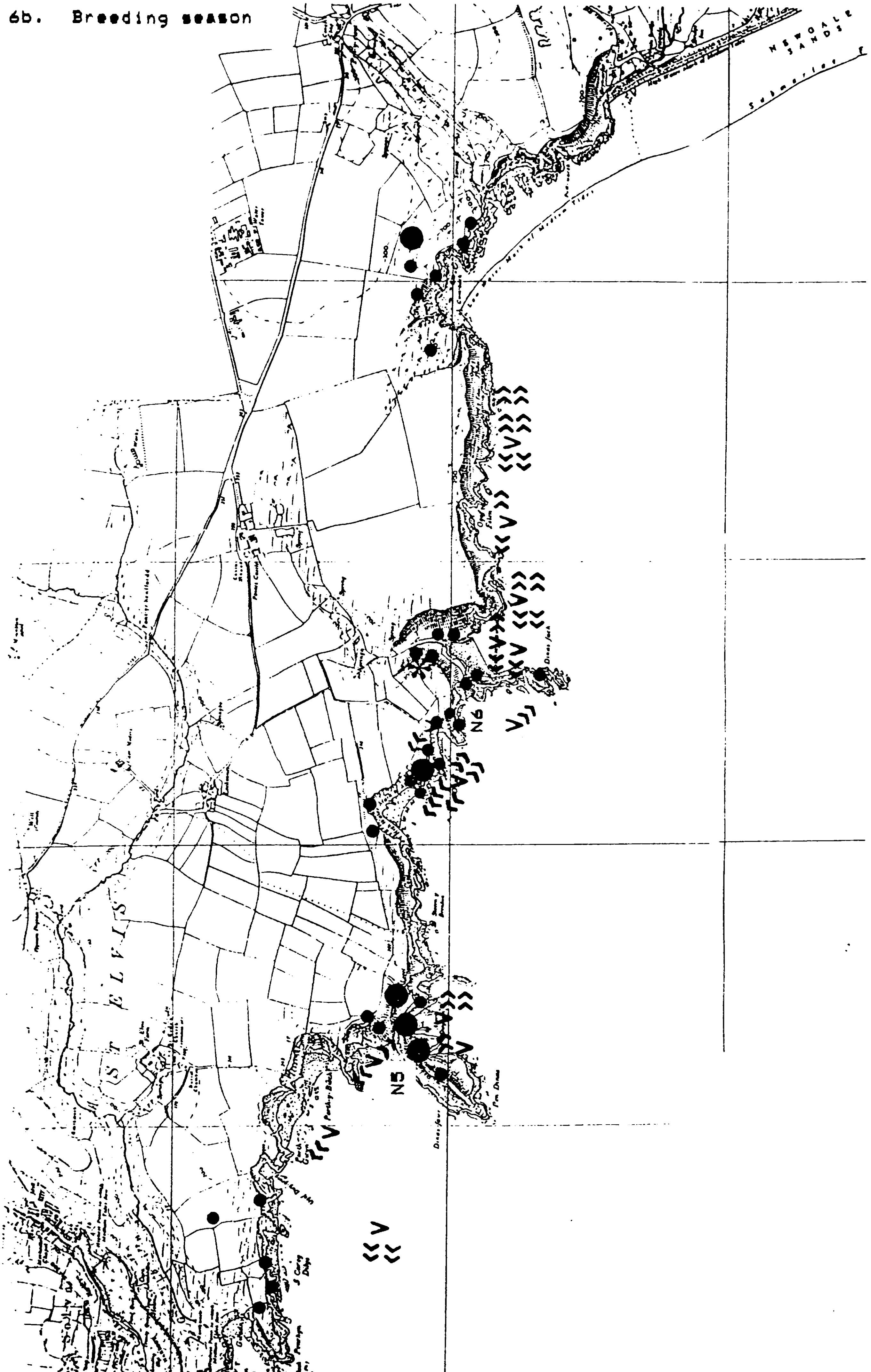

NEWGALE SANDS
N6
N5
ST ELVIS
Dinas Fach
Pen Dinas
Porth-y-Bwch

Fig. 6c. Post-breeding season

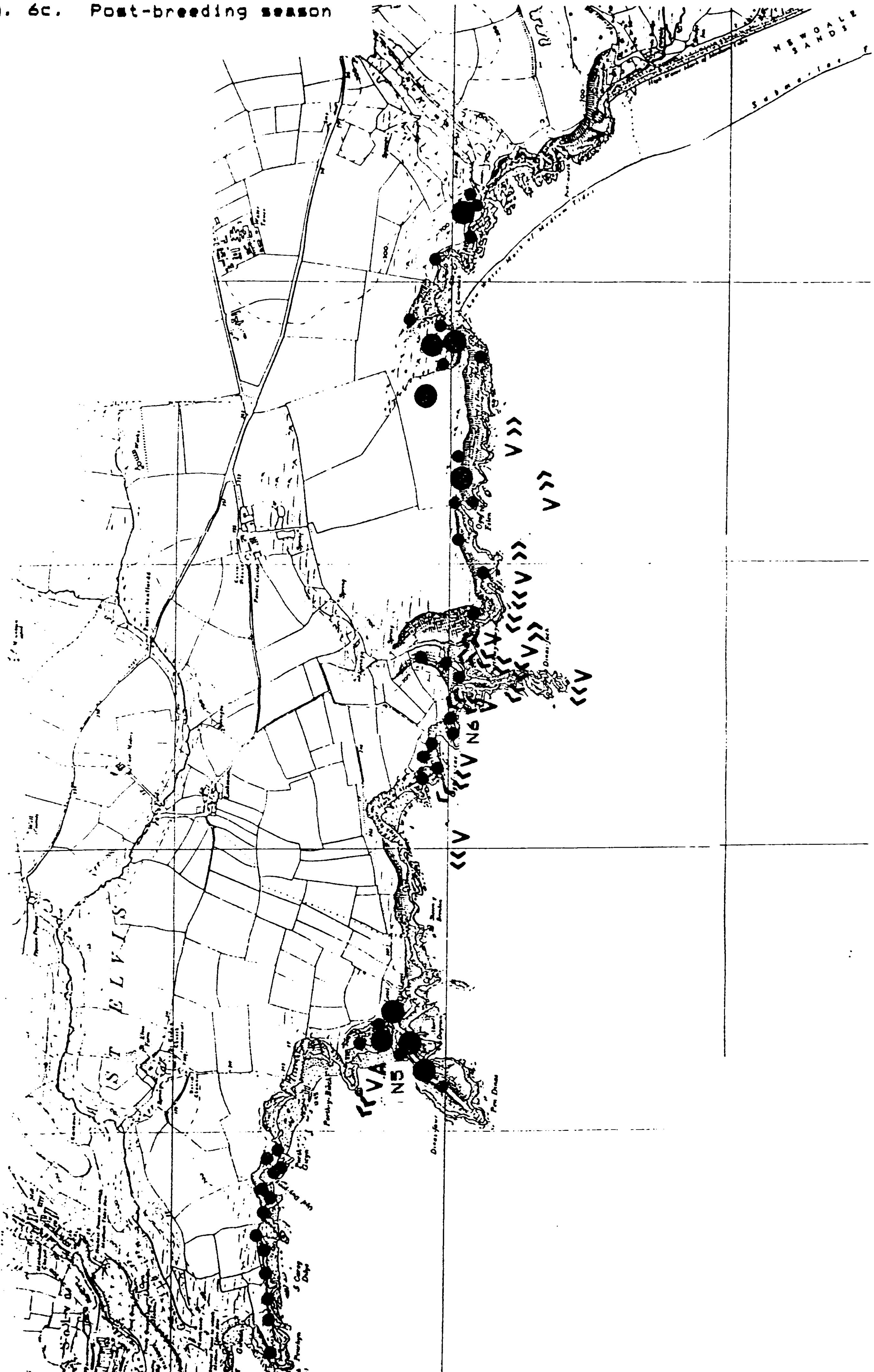

NEWGALE SANDS
ST ELVIS
N6
N5

Table 3. Chough diet in Study Area C as shown by faecal analysis (a), and the Scarabaeidae content (b). Figures are percentages of occurrences per faecal sample (a), and proportion in beetle positive samples (b).

Food	Winter	Breeding	Post-breeding	Year mean
(a)				
Beetles (all ages)	100	87.5	100	98
Earthworm	62.5	0	9	23
Cereal grains	19	0	15	14
Ants etc.	6	0	9	7
Fly larvae	0	12.5	6	5
No. faecal samples	16	8	33	57
(b)				
Scarab's (all ages)	50	57	28	41

NB. Incomplete results

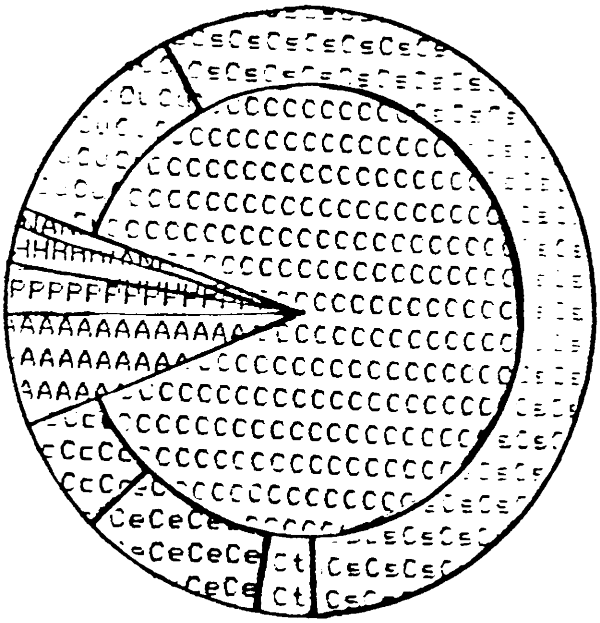


Fig. 7. Proportional selection of habitats by Choughs over one year in Study Area C with no. of FCM's. *See Methods for classification notes.*

Key		FCM's
Cu	Cliffs unspecified	541
Cs	Cliff-slope	2651
Ct	Cliff-top	149
Ce	Cliff-edge	455
Cc	Cliff-crevice	297
C	Cliffs (all)	4093
A	Arable	286
P	Pasture	136
H	Heath	87
AN	Ants	34
	Total	4636

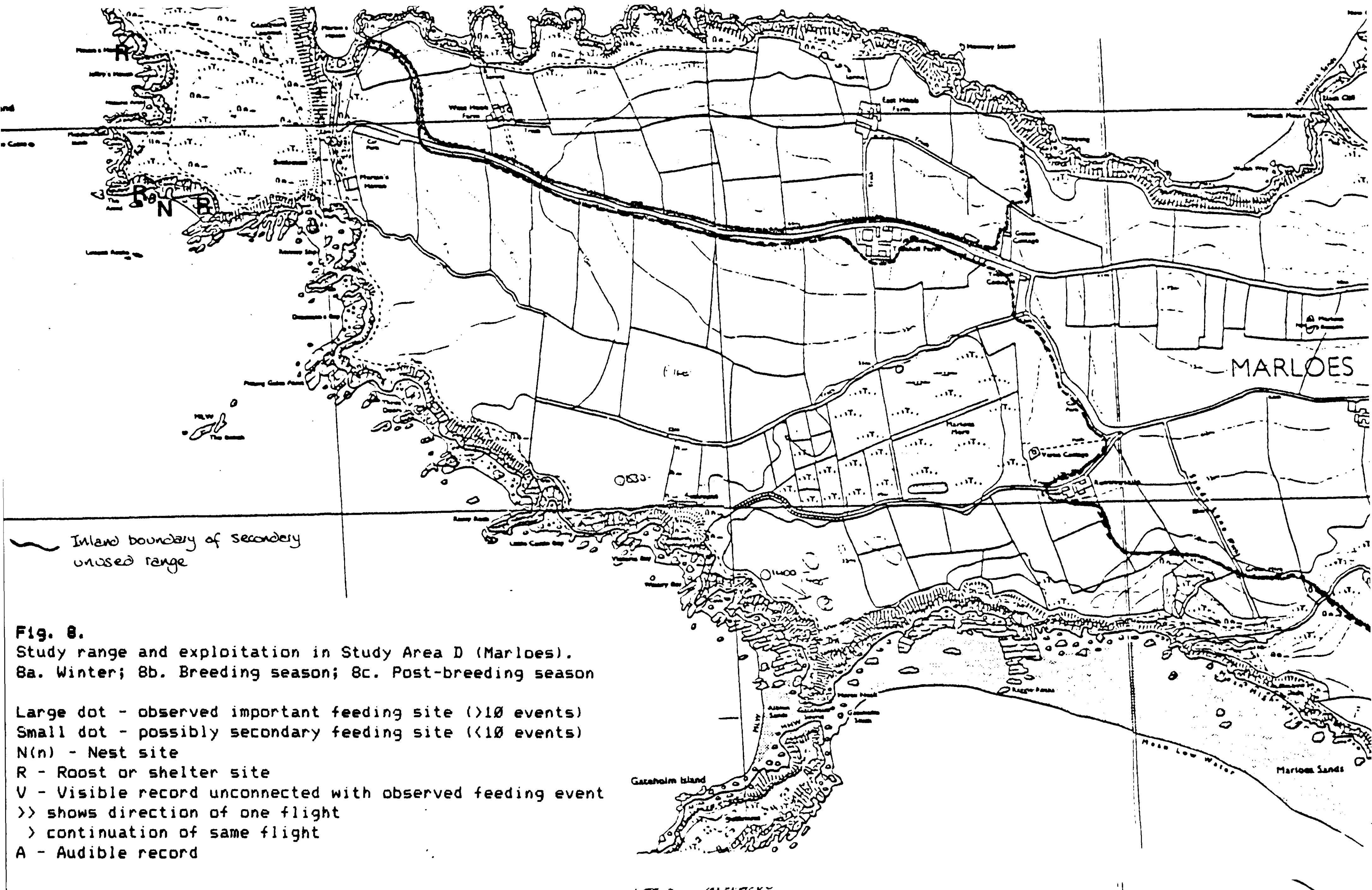
Compared to Sites A & B, the coastline between Solva and Newgale borders a hinterland more typical of modern agricultural systems. The traditional mixed farming of Cemaes and the diversity of Strumble are replaced by a considerable amount of improved pasture and intensive arable production. However, good habitat does exist, notably the grazed cliff pastures between Dinas Fawr and Gribbin Point, the excellent steep cliffs below them, the cliffs and slopes around Dinas Fach, the clifftop ecotones between here and the particularly important heathy hill rich in ants immediately west of Cwm-bach. This hill includes much gorse but the south-facing section is retained in a valuable open condition by rabbit grazing and possibly the actions of the ants themselves. These were the principal feeding sites and together they accounted for >90% of FCM's (>95% including cliff associated ant-feeding). The low importance (unsuitability?) of the farmland is suggested in Fig. 7. Stretches of the coastal slope are scrub influenced but appear to retain a sufficiently useful open state by virtue of intermittent grazing by wild and domestic herbivores, exposure, rocky outcrops, heath and ant activity. No wall-feeding was observed maybe due to more readily alternatives (see Future Plans).

Thus a combination of steep cliffs, a heavily indented coastline with two significant promontories all severely affected by (and therefore, of course, to the lee, protected from) climatic exposure, and a mountainous cliff-path which tends to deter all but the more committed walker, creates favourable conditions for Choughs. The quality of the cliff slopes and particularly of the Cwm-bach hill should be retained.

The two pairs (N5 & N6) which nested in 1988 produced 4 and 3 young respectively. Subsequent sightings, until at least February 1989, often of 11 birds (and on one occasion up to 18) suggest that all might well have survived. Such flocking seemed to continue the inter-brood mingling of the nest vacation period, although, in the absence of a colour-banding programme, relatedness has to remain speculative. Earlier during the breeding season the two pairs were often seen to associate and certainly they shared resources. The pattern of diet here over the year resembles Study Areas A & B, with a high emphasis on coleoptera; earthworms and cereals combining to show fairly high values (Table 3).

Study Area D: Marloes Peninsula

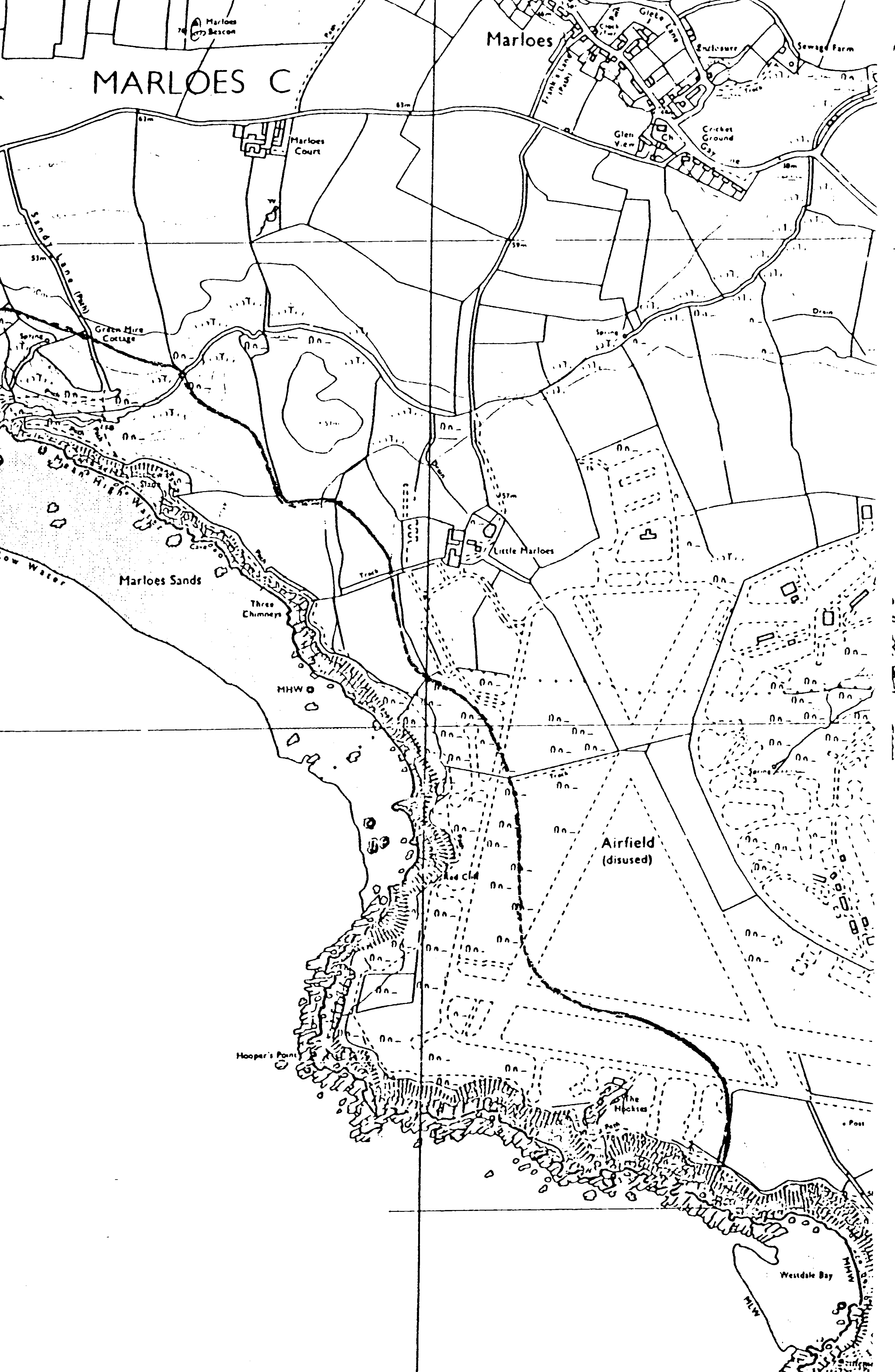
The Marloes peninsula (Fig. 8) at the extreme southwest of Pembrokeshire is adjacent to Skomer Island. It is largely improved agriculture except for the notable 'Deerpark' (a National Trust managed property with a resident breeding pair of Choughs (N7) which failed to reproduce in 1988) and the sheep-grazed cliff-slopes towards Westdale (see Fig. 8bb) - both important feeding grounds at opposite ends of a range of about 6.5km. Sightseers disturbed the Deerpark Choughs frequently especially while they tried to rest or feed near the nest. In co-operation with the National Trust and Pembrokeshire Coast National Park steps have been taken to reduce this in 1989.


MARLOES
Marloes Sands
Gateholm Island
East Hook Farm
West Hook Farm
R
N
R
R

Inland boundary of secondary unused range

Fig. 8.
Study range and exploitation in Study Area D (Marloes).
8a. Winter; 8b. Breeding season; 8c. Post-breeding season

Large dot - observed important feeding site (>10 events)
Small dot - possibly secondary feeding site (<10 events)
N(n) - Nest site
R - Roost or shelter site
V - Visible record unconnected with observed feeding event
>> shows direction of one flight
 > continuation of same flight
A - Audible record


Marloes Beacon
MARLOES C
Marloes
Glebe Lane
Enclosure
Sewage Farm
Frank's Lane (Path)
63m
Marloes Court
Glen View
Ch
Cricket Ground
Sandy Lane (Path)
53m
59m
Green Mire Cottage
Spring
Drain
51m
57m
Little Marloes
Track
Mean High Water
Marloes Sands
Low Water
Cave
Three Chimneys
MHW
Airfield
(disused)
Red Cliff
Hooper's Point
The Hookses
Post
Westdale Bay
MLW

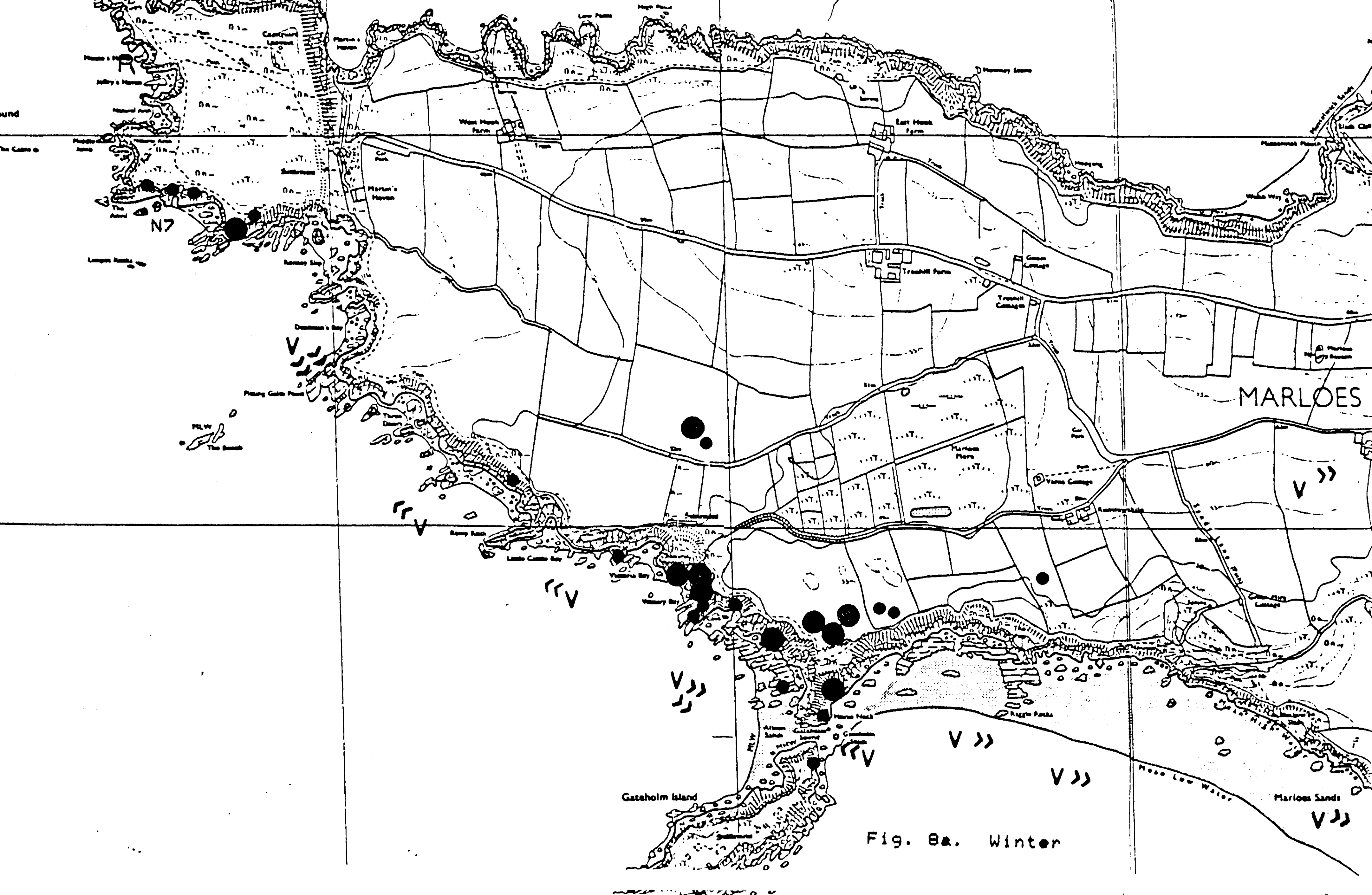

MARLOES
N7
R
Gateholm Island
Marloes Sands
Mean Low Water
Trehill Farm
East Hook Farm
West Hook Farm
Marloes Mere
Gateholm Sound
Albion Sands
The Smith

Fig. 8a. Winter

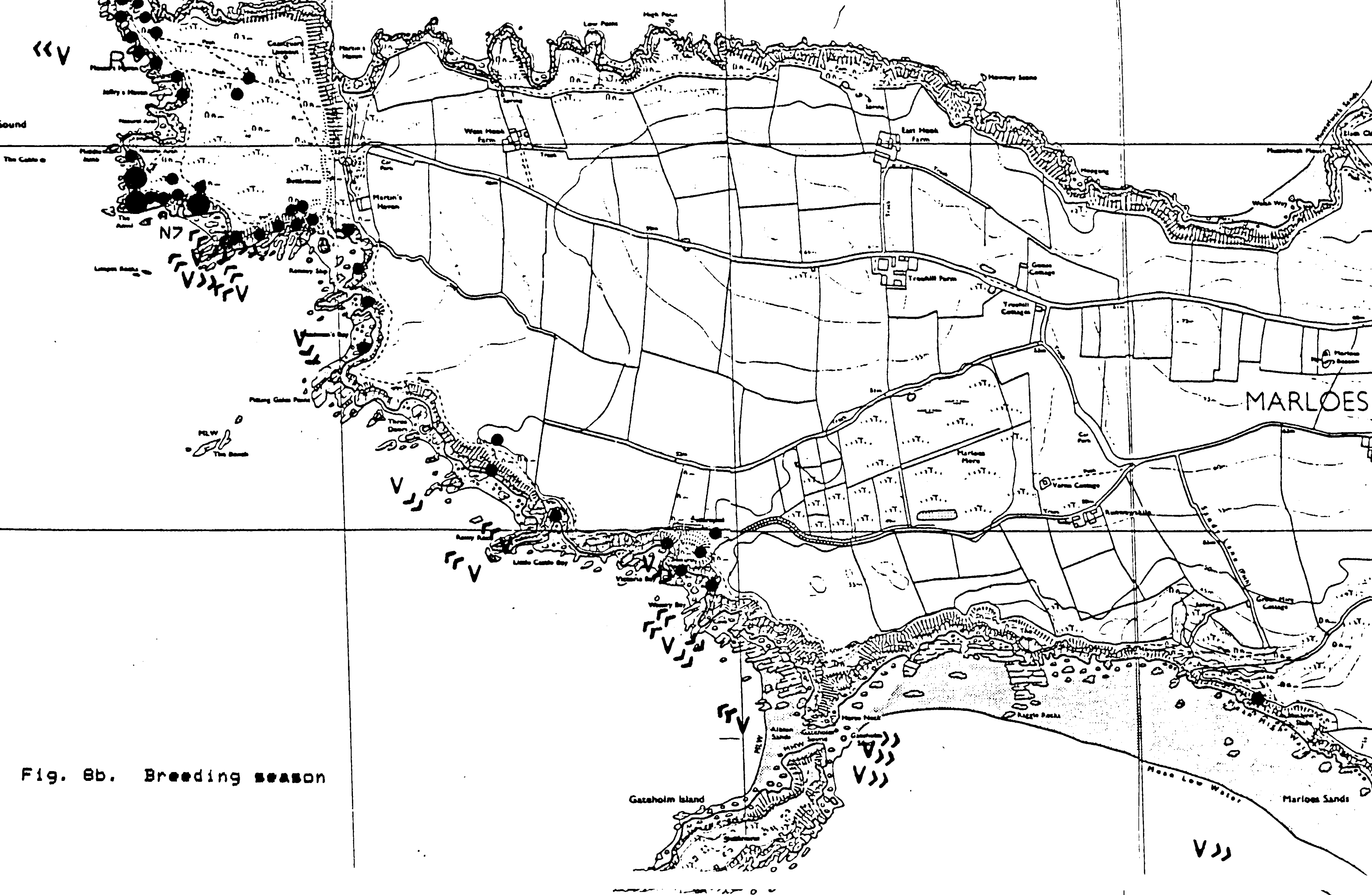

MARLOES
Marloes Sands
Gateholm Island
Martin's Haven
West Hook Farm
East Hook Farm
Trehill Farm
Marloes Mere
Victoria Bay
Little Castle Bay
The Deep
N7
R
V

Fig. 8b. Breeding season

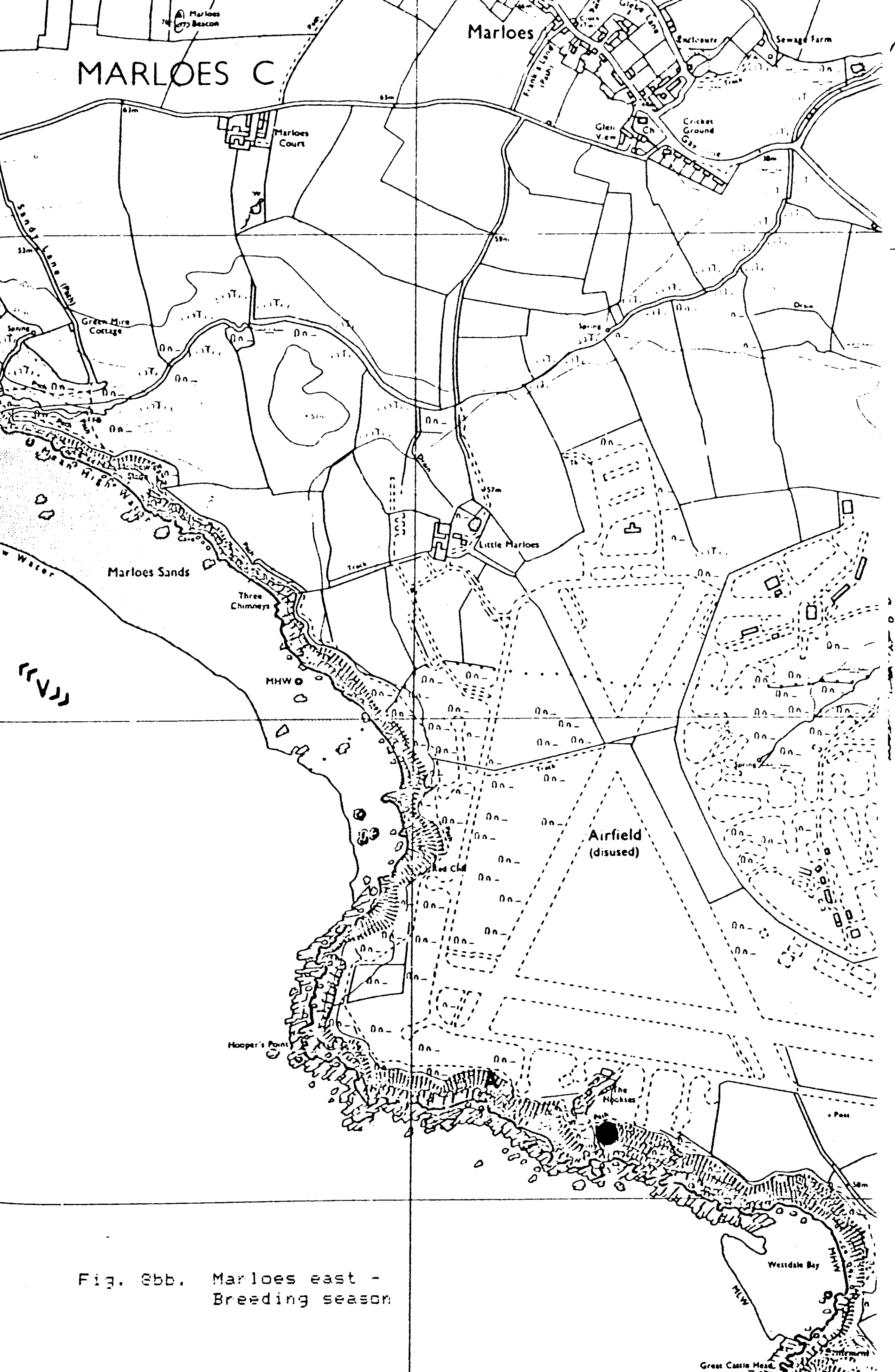
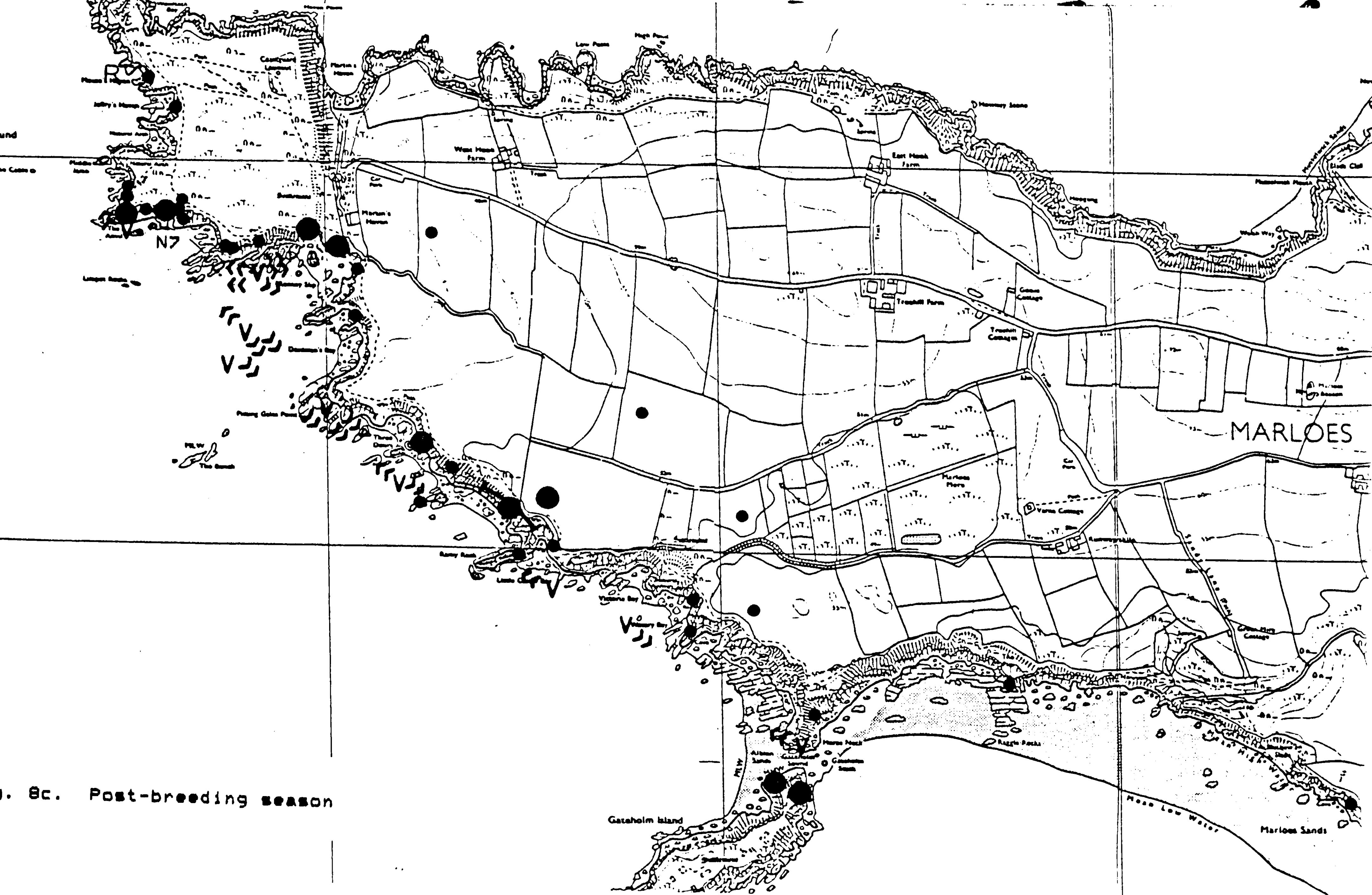

Marloes Beacon
MARLOES C
Marloes
Glebe Lane
Enclosure
Sewage Farm
Marloes Court
Cricket Ground
Glen View
Ch
Sandy Lane (Path)
Green Mire Cottage
Spring
Drain
Mean High Water
Marloes Sands
Three Chimneys
MHW
Little Marloes
Track
Airfield
(disused)
Red Cliff
Hooper's Point
The Hookses
Path
Post
Westdale Bay
MLW
MHW
Great Castle Head

Fig. 8bb. Marloes east -
Breeding season


MARLOES
N7
Marloes Sands
Gateholm Island
Mean Low Water
Marloes Mere
West Hook Farm
East Hook Farm
Trehill Farm
Albion Sands
Victoria Bay
Three Chimneys
The Anvil

. 8c. Post-breeding season

Table 4. Chough diet in Study Area D as shown by faecal analysis (a), and the Scarabaeidae content (b). Figures are percentages of occurrences per faecal sample (a), and proportion in beetle positives (b).

Food	Winter	Breeding	Post-breeding	Year mean
(a)				
Beetles (all ages)	59	100	100	68
Cereal grains	74	0	0	58
Earthworm	15	9	50	15
Fly larvae	2	27	0	7
Woodlice	9	0	0	7
Ants etc	4	0	0	5
No. faecal samples	46	11	2	59
(b)				
Scarab. beetles	63	9	100	50

NB. Incomplete results. Investigation pending on a further 13 samples

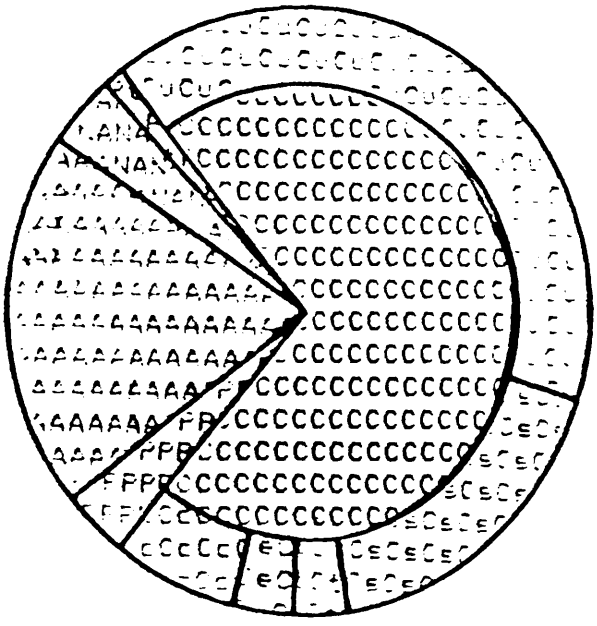


Fig. 9. Proportional selection of habitats by Choughs over one year in Study Area D with no. of FCM's. *See Methods for classification notes.*

Key		FCM's
Cu	Cliffs unspecified	2553
Cs	Cliff-slope	1133
Ct	Cliff-top	199
Ce	Cliff-edge	200
Cc	Cliff-crevice	468
C	Cliffs (all)	4553
A	Arable	1288
P	Pasture	235
AN	Ants	258
Pt	Paths	78
	Total	6412

Marloes supported a small flock of presumably non-breeding birds - regularly nine (including presumably the breeding pair) - throughout the winter of 1987/8 with up to 18 seen the following year. The improved agriculture seemed to affect the Choughs' behaviour, and their usage of arable land was greater at Marloes than elsewhere (Fig. 9). Usage of cliffs was also high (>70%) - indeed only exceeded in Study Area C.

Winter stubble feeding was here first identified south of the Hebridean island of Islay where it is common (Warnes, 1982). Otherwise the diet of these birds again showed dependence on beetles, earthworms etc (Table 4). The increased availability of cereal at Marloes due to sympathetic farming (spilled and subsequently sprouting grain left in situ) suggests that, outside the breeding season, the earthworm component might be determined by the availability of more preferred protein sources (Table 5).

DISCUSSION

The purposes of the project was to identify those elements of the Chough's autecology in West Wales which are important to its future conservation. I proposed to do this by firstly selecting certain key areas from the historic record and past surveys and censuses. Within these, the 'functional units' (Bignal et al., 1988) essential to the Chough's future viability were to be studied and their components better understood. Their relevance to Cornwall is not considered here.

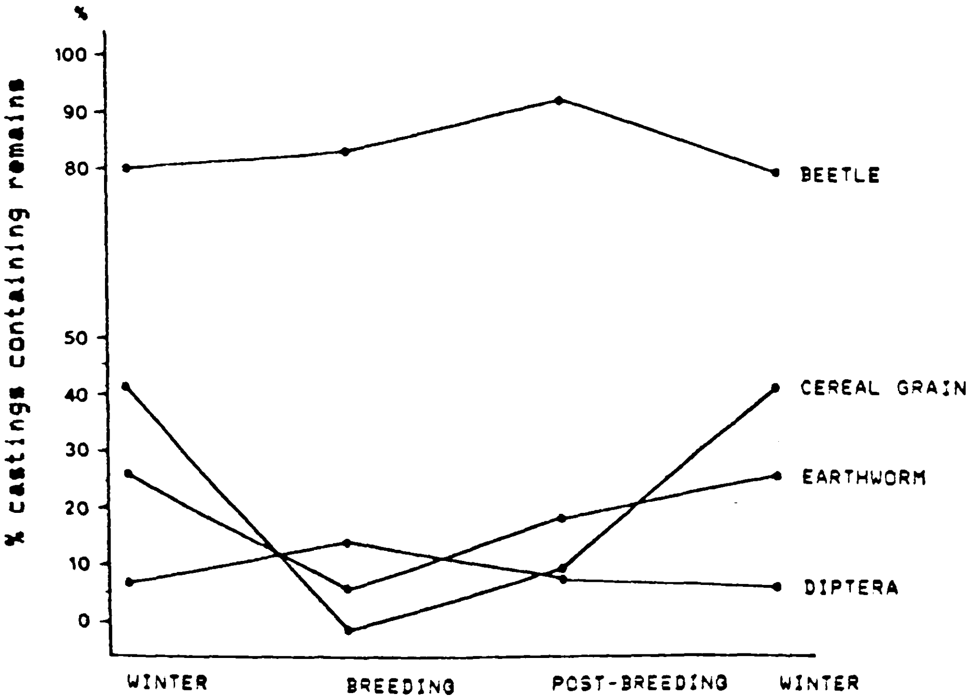
Diet

Looking at the dietary selection of the Chough through the year, which, of course, in turn closely reflects its habitat selection, the seasonal influence is clearly seen (Fig. 10).

The Chough's preference for insectivorous food is well known and supported by this study. The abundant, diverse and extremely widespread order Coleoptera (both larvae and adults are preyed upon by Choughs) are of fundamental importance with few, if any, of the main Chough habitats not represented by one or more species; cliff crevices being a possible exception. Assessed by faecal analysis, beetles are important in all study areas and in all seasons: never falling below 50% of the aggregated occurrences of detectable food remains except during the winter at Marloes, Study Area D (36%), where stubble-feeding was extensive. 'Scarab' (dung) beetles are the most important single family, averaging about half the total occurrences. (These aspects of the work are still in progress.)

Caution must be exercised when assessing prey spectra by faecal analyses due to a known under-representation of soft-bodied taxa such as the larvae of tipulid craneflies or 'leatherjackets' (Tipula spp.). This problem can be alleviated by differential diagnosis such as mentioned under Methods in connection with earthworm chaetae. To illustrate the problem, beetle parts (especially the elytra of Aphodius spp.) are distinctive and persist in an easily recognisable form. One of the most

Fig. 10. Annual diet of the Chough in West Wales as shown by faecal analysis from the four Study Areas pooled to give generalised results. Note: these results do not include ant content; soft-bodied prey (eg. diptera) which seldom show in evidence will be under-represented.



difficult groups is Diptera larvae: only occasionally do the skins survive, although in the absence of earthworm chaetae, a background matrix of earth with some cellulose material, led me to suspect that the bird had been feeding on Tipula larvae which were very common in Chough feeding ranges throughout the year. Faeces with such complete skins have helped confirm this supposition. Feeding trials are being undertaken to resolve similar questions.

It is possible that earlier investigations into Chough faeces overlooked earthworm chaetae due to the need for differential diagnosis. It is apparent from this study and an earlier inquiry in Cornwall that earthworms might be a vital dietary component (Meyer, in prep.). They might be used in the absence of a preferred energy source such as cereal grain. There is no doubt that stubble is an important resource beginning in late summer and continuing until exhausted. When grouped together over the two non-breeding seasons, earthworm and cereal evidence tend to complement each other (Table 5). Earthworm range 9.1-62.5%, cereal range 5.5-42.0%, grouped 24.8-31.0%. By season, the combined quota increasing from 29.4% in the post-breeding season to 69.7 in the winter.

Table 5. The relationship between earthworms and cereal grain in the diet of the Chough. Figures are percentage occurences per faecal sample in all Study Areas during non-breeding seasons for which reasonable sample sizes exist.

	STUDY AREAS						
	Post-breeding		Winter				Total
Food item	A	C	A	B	C	D	
Earthworm	9.7	9.1	33.3	56.25	62.5	15.2	31.0
Cereal	29.0	15.15	5.5	6.25	18.75	42.0	24.8
No. faecal samples	18	33	31	16	16	46	160

As mentioned under *Methods*, only a crude quantification of dietary components has been attempted at this stage since it is assumed that a simple presence or absence index related to known population dynamics of various key invertebrates and site/habitat descriptions already in existence will provide sufficient information to assist broad conservation planning.

The migration to cliff nesting sites during March involves a dietary switch away from pastoral and arable elements to a concentration on coastal insects. It is most likely that the switch is governed by the nutritive demands of egg production and rearing nestlings, for the parents either feed in the close vicinity of the nest, as at Cemaes (N2) or will make quite long journeys, as at Strumble (N3), *along* the coastline and not inland. The breeding season coincides, of course, with peak production and activity of prey taxa such as ants (Formicidae), which suddenly become very important. Choughs spend much time feeding in ant-rich sites such as coastal slopes and old or unploughed pasture and heath, usually grazed by domestic livestock (usually sheep) and sometimes by rabbits. *Lasius flavus*, *L. alienus* and *Myrmica ruginodis* are plentiful. Along with the adult workers, cocoons and presumably queens are sought together with woodlice, beetles and other symbiotic or cohabiting taxa. During the mild winter of 1988/9, Choughs were feeding on ants by February.

Habitat Requirements

As has been shown, Choughs migrate to breeding stations in March. This appears to be the only non-climatic induced disruption in their year - the return to a more mixed foraging after breeding happens more gradually and is dependent on the prevailing weather conditions. Grain left in fields after harvesting is eagerly sought but in the abnormally mild winter of 1988/9 inland fields were utilised little compared to the previous more typical winter. I will quantify this further in the course of my own work although if Choughs are as opportunistic and climate dependent as seems likely, a longer term study is needed.

Meanwhile, there arises a clear and well-defined need for a mixed agriculture well represented by pastoral elements and non-intensive cereal production. Where the existing cliffscape combines extensive therophytic zones, eroded open ecotones between clifftop vegetation and cliff-faces, and the earth/therophyte/rock interfaces which are rich in invertebrates, the semi-natural coastal grass-slopes and heath bounding an agricultural hinterland might be somewhat less important for Choughs. The coast between Solva and Newgale (see Study Area C under Results) is cited in support of this view. Thus, other conservation demands could possibly over-ride Chough requirements under these circumstances although it must be stated that the presence of herbivores on cliffs will always be beneficial to Choughs and the majority of invertebrates on which they depend. Prey taxa, especially ants (of vital importance), which cross over such boundaries are vulnerable and possibly of key significance.

There appears, in summary, to be a three-point requirement with 1 and 2 being optimal (see Conclusions):

1. Sympathetic non-intensive mixed agriculture on coastal fields, combining pastoral and arable elements - essentially cereal - with grazed hedgebanks preserved;
2. Suitable cliffs in association with promontories, headlands and/or frequent indentations comprising exposed earth, open low vegetation (therophytic) and abundant rock/earth interfaces either as strata, outcrops or in pockets; and
3. Semi-natural ground between 1 and 2 comprising either grazed or otherwise open (eg. exposed) low profile maritime grass or heathland.

Disturbance

Evidence from Mwnt and Marloes (N1 & N7), and observations of behaviour at Cemaes and Strumble (N2 & N3), suggests a nest-site territory vulnerable to disturbance within a 50 metre radius and possibly of crucial importance to successful reproduction. The Chough's preference for promontories as nesting-bases in this study is marked: all seven sites being thus associated. Promontories (and islands) have some functional advantages, as already mentioned, and form an identifiable discrete location. Unfortunately, people are also attracted to such viewpoints, and this inevitably causes disturbance (albeit benign), which might well, without control of access from March to July damage survival prospects. It will be interesting to monitor the experiments at Marloes Deerpark (N7) to see whether markers and notices deter curious sightseers and benefit the Choughs.

Serious disruption from other wild species was confined to one site (N3), where Peregrines nesting on the same cliff were seen to harass the Choughs. These Choughs did not reproduce successfully. Otherwise, occasional interactions with other corvids occurred at all sites. During the winter, Choughs were troubled by Ravens (Corvus corax) and Carrion crows (C. corone). Interestingly, as spring progressed roles became reversed and Choughs became more assertive and/or their adversaries less so. Only Carrion crows were a serious nuisance, sometimes with all-out attacks from 100 metres or more distant. Their attacks appeared deliberate and pre-emptive and caused the Choughs serious alarm. Ravens, on the other hand, made slower and more circumspective approaches and though eliciting evasive action caused less alarm and were avoided with no apparent difficulty - the Choughs sometimes mobbing the Ravens and making counter-attacks. Ravens appeared to be more of a nuisance than a threat, although this aspect of the study has yet to be fully analysed. No serious interactions with Jackdaws (C. monedula) or Rooks (C. frugilegus) were observed despite high numbers in some breeding ranges (eg. N6).

Starlings (Sturnus vulgaris) also occasionally plagued Choughs during the winter, particularly at Marloes. Flocks of many hundreds would follow the Choughs possibly using them as food guides, at times this seemed to cause the Choughs to vacate feeding sites.

MANAGEMENT CONCLUSIONS

Partly as a result of the work in hand and partly as a result of other work (eg. Moore, 1966; Bullock, 1980; Warnes, 1982; Bullock et al., 1983; and Bignal et al., 1988) we can begin to arrive at management recommendations for this species. The following are identified with West Wales in mind although they are probably also applicable elsewhere.

1. Traditional mixed farming.

Develop pastoral farming utilizing semi-natural coastal grassland, permanent pasture and older term leys at sufficient stocking rates - where this will not conflict with other conservation requirements - to create poached and eroded earth patches with concomitant manure and short grass (<2cm).

Arable elements, particularly cereals of which at least part of the product is accessible to the Choughs as grain left to mature naturally or as stubble residue.

2. Associated semi-natural features.

Conserve invertebrate communities, especially ants, and encourage rabbit populations. Conserve areas of outcropping rock in grazed vegetation over shallow earth. Promote paths where appropriate: wider paths giving trampled, open vegetation with eroded zones are preferable to narrow heavily eroded trails between long vegetation.

Prevent further increase of closed scrub and maintain open vegetation on coastal slopes, preferably by mixed livestock at appropriate stocking rates to create conditions as in 1) and/or by mechanical means as currently employed at Cemaes.

Maintain grazed wallbanks. To allow grazing and provide Choughs with valuable vantage points, single summit fencing on walls is preferable to fencing at their bases on both sides.

3. Prevent disturbance.

Particularly within a 50 metre radius of occupied nest sites. Provided there is suitable support-ground elsewhere, such as out of human sight (eg. inaccessible cliffs) or >75-100m away from visible presence, coastal footpaths may not damage Chough interests, and, as pointed out in this report, could actually be a benefit.

4. Prevent further non-fragmentation and isolation of ranges.

A continuity of habitat with adequate support-ground (see Bignal et al., 1988) is probably necessary for long-term viability.

5. Offshore islands and mainland promontories.

These are key habitats and should be optimised wherever possible by reference to the foregoing.

FUTURE PLANS

Further work is still in progress as part of my Ph.D project. A considerably fuller report on this area can emerge in due course (approx. one year) in which I will be able to incorporate much of my own project work, thus supplementing this one.

Subjects to be covered in more detail will be:

1. The dependence of Choughs on 'micro-habitats' (ie. pockets of exposed substrate, linear paths, rock/vegetation interfaces, walls, ants, shelter and aspect etc). Multi-regressional techniques will be employed in an attempt to understand more fully the inter-relationships between Choughs and these separate featuresand their own inter-effects.
2. Invertebrate and habitat availability - based on my earlier survey currently being digitised - will be correlated using similar techniques. FCM's will be correlated to this availability.
3. 'Feeding exhibits': all confirmed Chough feeding incidents, such as direct observation, results from the 'Feeding Inquiry' exercise, prey site sampling, and faecal analysis - all these exhibits will be inter-related, and again through non-parametric methods analysed for significance to Choughs.
4. Faecal analysis is only half completed, Dr Paul Buckland of Sheffield University is helping on fragment identification and currently holds the majority of faecal remains including ants.
5. Feeding efficiencies in different habitats, assessed by analysis of focal period observations.
6. All disturbance incidents and interactions (inc. with humans) will be analysed and assessed in an attempt to evaluate their impact on feeding and breeding birds.
7. Tithe map analysis of the 1840s. The counties of Pembrokeshire and Cardigan will be digitised in the same way as already accomplished for Cornwall and computer analysed. This will provide useful historical baseline data, with replicable methodology, from which modern land use trends may be monitored.

NB. Appendices will be produced in respect of 1, 2, 3, 4, 5 & 6.

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Finally, I must express my deep gratitude to my main sponsor in Cornwall, Mike Reynolds, Director of the Rare and Endangered Birds Breeding Centre at Hayle, without whom the whole project would probably have foundered, and who has enabled much of the extra work to go ahead which I hope will benefit the Choughs of West Wales as much as any future residents in Cornwall.

APPENDIX IX

The predictability and patterns of vigilant behaviour

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Abstract

While foraging, many animals alternate between feeding and scanning. Spectral analysis of continuous series of scan durations S and inter-scan intervals I for American Goldfinches *Carduelis tristis*, feeding either on small or large seeds, and choughs *Pyrrhocorax pyrrhocorax* showed that there were nonrandom fluctuations in the magnitude of S and I in all the examined series. Both the I and S showed cyclical oscillations between short and long events. Within individuals the sequential and temporal patterns in the I and S series were similar. However, the temporal patterns were more affected by variations in food-handling time than were the sequential ones. The predictability of the I and S series and the similarity, within individuals, of their sequential and temporal patterns seem general processes resistant to variations in behavioural constraints, and the temporal patterns in the I and S series fit to the method of handling food.

Key words: Vigilance; Scanning pattern; Spectral analysis; Cyclical oscillation; Bird

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1. Introduction

Recent studies of solitary foraging purple sandpipers *Calidris maritima* and Barbary doves *Streptopelia risoria* (Desportes et al., 1989; in press a and b) demonstrate discrepancies between observed scan durations S or inter-scan intervals I (the delay

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between an animal putting its head down to feed and the moment when the head is raised again) and those predicted by previous theories. For instance, it has been stated (e.g. Pulliam, 1973; Caraco, 1982; Pulliam et al., 1982; Hart and Lendrem, 1984; Lima, 1987) that scans are instantaneous and that the I should be unpredictable in length to "prevent any attempt by the predator to predict the duration of inter-scan interval during which it might make its final uncovered hunting approach" (Lendrem et al., 1986). However, spectral analysis of series of I and S (which are of finite and variable duration; e.g. Elgar and Catterall, 1981; Cezilly and Brun, 1990) have detected non-random sequential and temporal patterns in all the examined series. Both the S and I showed rapid cyclical oscillations between short and long events (Desportes et al., 1989; in press a).

Here we analyse data on vigilant behaviour of American goldfinches *Carduelis tristis* and choughs *Pyrrhocorax pyrrhocorax* to study the effects of endogenous and exogenous behavioural contraints on the predictability of S and I series and the similarity of their sequential and temporal patterns.

Methods

Data collection

A continuous sequence of 60 S and 60 I was obtained from each of 33 American goldfinches videotaped while foraging in flocks (of up to 70 individuals) on a feeder (Popp, 1988). Data were obtained for 18 birds (GN 1 to GN 18) when the feeder was stocked with small niger seeds (mean size: 1 × 5 mm; mean handling time: 0.12 s) and 15 birds (GS 1 to GN 15) when it was stocked with large sunflower seeds (mean size: 6 × 12 mm; mean handling time: 1.45 s).

We also obtained a continuous sequence of S and I from each of 5 choughs referred to as CH 1 (46 S and 46 I), CH 2, CH 3, CH 4 (64 S and 64 I) and CH 5 (42 S and 42 I). These data were obtained by recording observations onto audiotape (for later transcription) of the foraging behaviour of each chough while it was feeding in groups (of up to 3 individuals) on invertebrates, generally below the level of the substrate (i.e. digging).

Data analyses

We conducted spectral analysis, applied here as described in some detail in Desportes et al. (1989), to test for the predictability of individual S and I series. For a series of N events, each having an order of occurrence X_i ($i = 0$ for the first event), spectral analysis estimates the proportion g_J of the total variance in the series explained by the periodic components. These components are the harmonics ($J = 1, 2, \ldots, N/2$, where each J measures the number of times a cycle is repeated in the entire series) and the corresponding periodicities (N/J). Confidence intervals calculated for g_J identify statistically significant values greater than the 95% upper confidence limit.

The cycles in the individual I and S series are identified from the peaks, where a peak is defined as an event longer than both its predecesor and successor. The mean distance (in X_I units) Δ_I or Δ_S between successive peaks and the mean duration (s) or D_I or D_S of the cycles (from the offset of a peak to the offset of the next one) measure respectively the sequential and temporal patterns in the series.

Results

For each bird, the sum of the significant g_3 values in the I and S series accounted for substantial proportions of the explained variance, such that all series contained significant non-random fluctuations in magnitude (Table 1). There was no significant difference between the sum of the significant g_3 values in the I and S series within individuals (Wilcoxon test; $z = 0.46$; $p > 0.05$). Disregarding long-term periodicities (resulting usually from longer I at the beginning of the series and longer S at the end of the series), the predictability of the I and S series is related to short-term periodical fluctuations. Both the I and S oscillated in cycles between short and long events (troughs and peaks), interspersed with events of intermediate duration. The sequential or temporal patterns in the I and S series are similar within individuals (Table 1): neither Δ_I and Δ_S nor D_I and D_S differ significantly (Wilcoxon test; $z = 0.01$ and 0.11 respectively; $p > 0.05$). However, when comparing between individuasls, the temporal patterns are more variable than the sequential ones. The coefficients of variation (CV, the ratio of the standard deviation s to the mean m) for D_I ($s = 12.73$; $m = 19.96$; $CV = 0.64$) and D_S ($s = 12.03$; $m = 19.39$; $CV = 0.62$) are significantly greater (t statistic; Dawkins and Dawkins, 1973) than the coefficients of variation for Δ_I ($s = 0.80$; $m = 3.98$; $CV = 0.20$) and Δ_S ($s = 1.26$; $m = 4.06$; $CV = 0.31$): t ($df = 37$) $= 5.32$ and 3.90 ($p < 0.05$).

Discussion

The similarity between the GN, GS and CH data and the previous analyses (Desportes et al., 1989; in press a) in the results of spectral analysis, in the mean distances between peaks and in the mean durations of the cycles for the I and S series demonstrates that the non-random sequential or temporal patterns of feeding and scanning are not restricted to the particular species of bird examined previously (the purple sandpiper, PS, and Barbary dove, BD) or to individuals foraging solitarily. We have now shown there to be predictable patterns in feeding and scanning in a range of species foraging in a variety of context: social (GN, GS, CH) and solitary (PS, BD) feeding on dispersed (PS, BD, CH) and clumped (GN, GS) food resources, and exhibiting short (GN) and long (GS) food-handling times. Therefore, the predictability of the I and S series and the similarity, within individuals, of their sequential or temporal patterns, seem general processes.

These processes presumably confer anti-predatory benefits (Desportes et al., 1989; in press a). The avoidance of consecutive long I prevents an animal fron being surprised by predators (such as hawks) that usually do not stalk or ambush their prey. Lima (1987) and Kaitala et al. (1989) have emphasized the importance of intragroup behaviour on the trade-off between maximizing the rate of energy intake and minimizing the risk of predation for birds foraging in groups. Pulliam et al. (1982) have also discussed the possibility that birds in flocks would use a cooperative scanning

TABLE I

Results of the analyses of the inter-scan intervals (I) and scan durations (S) series for goldfinches feeding either on niger (GN) or sunflower (GS) seeds and choughs (CH). Values given are the proportion of the variance in the I and S series explained by significant periodicities (Σg_i), the mean duration (in s) of a cycle (D), and the mean distance (in X_i units) between successive peaks (Δ).

Bird		Σg_i		D		Δ	
		I	S	I	S	I	S
GN	1	0.50	0.67	7.02	5.80	4.17	3.40
	2	0.63	0.57	9.81	16.04	5.38	9.99
	3	0.68	0.54	7.33	7.69	4.73	5.00
	4	0.68	0.58	6.83	7.20	4.64	4.91
	5	0.45	0.56	9.47	7.43	5.40	4.27
	6	0.58	0.55	6.96	9.64	4.18	5.78
	7	0.60	0.44	8.01	5.98	5.00	3.71
	8	0.63	0.70	5.71	5.58	3.79	3.44
	9	0.55	0.51	6.77	7.48	4.17	4.67
	10	0.58	0.53	6.48	7.09	3.93	4.31
	11	0.47	0.73	5.68	8.38	3.44	4.91
	12	0.52	0.57	7.02	5.93	4.67	3.86
	13	0.65	0.60	7.23	6.78	4.33	4.00
	14	0.76	0.51	8.85	7.89	4.30	4.82
	15	0.62	0.62	9.28	7.73	5.40	4.50
	16	0.65	0.62	6.95	7.28	4.33	4.67
	17	0.58	0.49	10.47	7.48	6.11	4.38
	18	0.77	0.63	6.81	8.93	4.08	5.40
Mean		0.61	0.58	7.59	7.80	4.56	4.78
GS	1	0.66	0.69	41.37	45.39	3.86	4.25
	2	0.66	0.66	40.65	23.53	4.42	2.84
	3	0.58	0.58	32.91	27.76	3.79	3.19
	4	0.64	0.60	28.91	31.43	3.11	3.44
	5	0.57	0.60	29.74	34.26	3.35	3.85
	6	0.59	0.72	33.36	34.85	3.71	4.00
	7	0.71	0.63	25.24	30.42	3.06	3.67
	8	0.40	0.69	37.52	27.75	3.69	3.12
	9	0.56	0.54	33.13	29.96	3.64	3.24
	10	0.64	0.50	26.05	31.21	3.11	3.67
	11	0.53	0.58	25.99	28.51	3.25	3.86
	12	0.58	0.59	37.12	27.44	4.42	3.18
	13	0.66	0.61	39.16	37.56	4.15	4.00
	14	0.54	0.55	28.37	32.28	3.44	3.93
	15	0.55	0.63	30.01	21.82	3.57	2.75
Mean		0.59	0.61	32.64	30.94	3.64	3.53
CH	1	0.68	0.57	16.89	24.39	2.80	4.22
	2	0.55	0.71	30.96	34.17	2.76	3.16
	3	0.54	0.61	34.02	30.60	2.77	2.50
	4	0.58	0.61	24.22	20.35	3.21	2.68
	5	0.59	0.44	26.23	22.67	3.17	2.71
Mean		0.59	0.59	26.46	26.44	2.94	3.05

strategy, which implies that each flock member must monitor the behaviour of its flock mates in order to detect any defection in cooperative scanning. However, this strategy would result in an additional effort of scanning, as well as a considerable effort of memory. Therefore, the sequential and temporal patterns of scanning in groups might be a compromise between the need for unpredictability (to prevent predators timing their attacks) and the need for an economical system of mutual monitoring of scanning within the group.

Although similar within individuals, the temporal patterns in the I and S series are more variable between individuals than the sequential ones. The temporal and sequential patterns describe the I and S cycles at different levels of analysis: with or without reference to time. Sequence analyses of the peaks and troughs, interspersed with events of intermediate duration, measure the degree of redundancy or stereotypy (Baker, 1973; Dawkins and Dawkins, 1973) of the I and S series. The sequential patterns of feeding and scanning are very predictable, and less variable than the temporal ones. One interpretation of the functional significance of the high variability in temporal patterns is that foragers are responsive to variations in foodhandling time (Lendrem, 1983; Godin and Rangeley, 1989). For instance, goldfinches handling sunflower seeds (which requires manipulations in order to find the crack in the husk and break it open) have long I and S, low rates of feeding or scanning, and long D_I or D_S; conversely, when handling niger seeds (which only involves pecking at the seeds and swallowing them) they have shorter I and S (Popp, 1988), higher rates of feeding or scanning, and shorter D_I or D_S. Food-handling time thus constrains the durations, rates and temporal patterns of feeding and scanning, and these parameters fit to the food-handling method of the goldfinches.

In the absence of information about the probability of predator attack, our analyses do not reveal whether the observed patterns represent an optimal solution to the trade-off between maximizing the net rate of energy gain (a parameter affected by the time and energy costs incurred while handling food items; Godin and Rangeley, 1989) and minimizing the predation risk. The similarity of the patters in predictable I and S series suggests that it is necessary to elucidate the relationship between the I and S (for instance, by analysing the predation risk from the series of the ratio of each I to the S that precedes it) in order to study how prey animals eat without being eaten.

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APPENDIX X A captive feeding experiment

Introduction Although faecal analysis gives direct evidence of food intake, and is therefore a useful adjunct to examination of diet, caution must be exercised when attempting to use unvalidated data to quantify and qualify food intake. In this small experiment with a captive Chough, food selection and throughput, and energy intake were examined.

Methods The subject was a captive-bred bird, 31 months old, weighing at the beginning and end of the trial 300g (an average weight for the species; Section 1.3.1), and habituated onto an avicultural diet based on insectivorous 'softfood', mashed egg, raw meat and mealworm beetle *Tenebrio molitor* larvae. The limited time and facilities available reduced the amount of data that could be collected. Due to the time of the year (December), difficulty was experienced in finding sufficient quantities and varieties of prey, something at which wild Choughs are clearly more proficient than the observer! The subject was not fed on the day prior to the investigation. Earthworms used to measure the throughput of chaetae were boiled, finely cut and mixed with a small amount of favoured softfood, no more than would be taken in one session. The live food were presented simultaneously in a shallow dish.

Results Earthworm chaetae, from a single feed (one medium-sized worm, see Section 5.2.1), appeared in 12 successive faeces ($\bar{x}$ =1.75/dropping, ±1s.e. 0.58; Table 1). The first appearance after ingestion was 68 minutes, and the longest period to elapse before evidence ceased to appear was 315 minutes. Chaetae do not appear consistently within all samples: on day 2 of the experiment, between the first and last recoveries of 46 samples, there were 26 faeces (56.5%) in which no chaetae could be found.

Table 1 Recovery of earthworm chaetae from a captive Chough's faeces

Day	Time of feeding (GMT) and amount	Time of faecal collection	No. faeces			Chaetae	
			total	-ve	+ve	n	$\bar{x}$
1	1305-50; portions of 1 earthworm	1450	10	10	0	0	-
		1550	14	6	8	14	1.8
		1650	10	9	1	1	1.0
2	0845-46; 3 earthworms	0845	7	7	0	0	-
		0945	5	5	0	0	-
		1045	6	3	3	>30	10.0
		1145	11	3	8	17	2.1
		1245	10	7	3	3	1.0
		1345	9	6	3	3	1.0
		1445	10	7	3	3	1.0
		1545	10	10	0	0	-
		1645	10	10	0	0	-
3	0934-48; 1 large earthworm	1030	26*	26	0	0	-
		1050	4	1	3	6	2.0
		1105	3	1	2	4	2.0
		1120	4	1	3	5	1.7
		1135	5	1	4	6	1.5
		1235	9	9	0	0	-
		1335	9	9	0	0	-

* includes overnight droppings

In one short day (7.5hrs), the Chough consumed 61g of food, which converted to approximately 814.2kJ (271.4kj/100g^{-1} body weight; Table 2). This figure is considerably higher than the 157.8kJ/100g^{-1} estimated by Bullock (1980) as being the daily energy budget (DEB) of a 300g Chough but does not allow for non-assimilation. Taitt (1973) and Gromadzki (1979), both working on Starlings, estimate an assimilation rate of *ca.*75% (Taitt basing his estimate on a mealworm diet). A 75% assimilation on the above Chough intake would result in an energy gain to the subject of 203.6kJ/100g^{-1}. Against this must be weighed the reduced energy expended by a captive bird in searching for food which is available *ad lib.* Hogstedt (1981) estimated the DEB of a 200g Magpie at 315.0kJ/100g^{-1}, which is almost exactly double Bullock's estimate for a Chough.

Table 2 Energy intake of a captive Chough weighing 300g during 7.5 hour winter daylight period

Food	Approx. energy value (kJ/g^{-1})	Weight (g) offered	Weight (g) consumed	Approx. energy intake (kJ/g^{-1})
Cheese (grated)	17.6[a]	43	23	404.8
Tenebrio larvae	10.9[b]	37	34	370.6
Meat strips	9.7[a]	20	4	38.8
Totals		100	61	814.2

Sources: [a] Baker (1964), [b] Allchurch (1986)

Perhaps the results of this small experiment help to clarify the picture, allowing for the captive status of the experimental bird, but miscellaneous results illustrate the danger of trying to be too precise in calorific or energy requirement estimates, as Richford (1978) stressed. Individual prey organisms vary in body condition, age, sex and reproductive status, all of which affect fat resources and therefore energy content; moreover, fat content varies throughout life, and is a major potential source of error in energy budgets (Southwood 1968). Nevertheless, the consensus of opinion remains that calorific indices, and similar, remain the best available method, and the most easily recognised standard, of assessing dietary quality. Alternative methods would include analysing protein. No systematic difference between the two techniques, relative to protein and energy content of food exists (Linton 1927, McDonald *et al*. 1966). Fats contain about 2½ times as much energy as carbohydrates, the difference reflecting the the larger ratio of carbon and hydrogen to oxygen in the former (*i.e.* fats are in a lower state of oxidisation and are therefore capable of yielding more energy when oxidised). Protein has a higher gross energy value than carbohydrate. In spite of these differences, the predominance of carbohydrates in cereal food means that such food varies little in gross energy content. Only foods rich in fat will have proportionately high values.

The captive pedigree of the subject, the fact that only one individual was involved, and the limited choice of food items presented prevent conclusions from being drawn about prey preferences, except perhaps to note that woodlice were selected before any other uncustomary food (Table 3). The reluctance of Choughs to take entire earthworms in captivity has been noted by myself and other authors (*e.g.* Darke (1971)).

Table 3 Food selection and faecal evidence of a captive Chough

Food	Time (min's) before first selection	Time delay before appearance of faecal evidence	Faecal evidence
Mealworm (*Tenebrio molitor*) larvae	<1	85-145 min's	mandibles, leg parts
Cheese (grated)	<1	?	none
Woodlice	1-2	60-120	tergites & 1 complete exoskeleton
Millipedes	*ca*. 60	*ca*. 120	body segments
Earthworms (entire)	-	-	not selected
Centipede	-	-	not selected
Ants (red and black)	-	-	not selected